What is driving the range extension of *Gibbula umbilicalis* (Gastropoda, Trochidae) in the eastern English Channel?

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Submitted in partial fulfilment for the award of Master of Research (MRes)

awarded by Bournemouth University.

March 2016

Abstract

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What is driving the range extension of *Gibbula umbilicalis* (Gastropoda, Trochidae) in the eastern English Channel?

Until around 2000, the marine gastropod *Gibbula umbilicalis* (Da Costa 1778) was previously only present as far east as the Isle of Wight on the south coast of England. Since 2000 the range of *Gibbula umbilicalis* has extended 140km eastwards with records now present as far along the coast as Kent. Since the 1990s temperatures in the English Channel have increased faster (and to higher levels) than during any other period recorded. The importance of sea temperature driving the range extension of *Gibbula umbilicalis* has not been fully evaluated. Field and laboratory studies were carried out between March and September 2015 on populations at two long-established sites in the west of the Channel (Lyme Regis and Osmington) and two recently colonised (since 2000) sites in the east (Cuckmere and Eastbourne) to determine whether:

I. reproductive development and spawning was synchronised between different populations, and whether it was correlated to sea temperature;
II. there was evidence of recent recruitment at the “new” sites and if there was a difference in population structure at each location;.
III. new populations east of the Isle of Wight can now be considered established.

Reproductive development was positively correlated to sea temperature, however this was not synchronised between sites; populations at Lyme Regis and Osmington matured before Cuckmere and Eastbourne, although the differences were slight. By September, spawning had begun at the long-established (western) sites but not the recently colonised (eastern) sites. There was evidence of recruitment of a 2014 cohort at all sites. However, the number of juveniles observed was lower in the eastern Channel during spring (March-May) in comparison with western sites, but increased each month from June onwards. The later detection of juveniles in the east is attributed to delayed spawning and settlement. On the evidence of continuing reproductive development and recent recruitment, populations at Cuckmere and Eastbourne can now be considered established. Their proximity to the continent exposes them to colder winters which may intermittently increase mortality. However, it is considered that these populations are now sufficiently large to withstand all but extreme events.

The range extension of *Gibbula umbilicalis* in the eastern English Channel is attributed to multiple factors related to increasing temperatures. Higher summer sea temperatures are likely to have accelerated gonad development and spawning at the previous range limit. This provided juveniles more time to mature before temperatures fell during winter. Increased size/fitness limits winter mortality and promotes recruitment, resulting in growth of the range-edge populations. The larger breeding population resulted in an increase in larval supply, allowing the barrier at the range-limit to be penetrated and new sites seeded. The annual sea temperature increases will have had the same effect on the new arrivals settling in the eastern Channel; recruitment at levels exceeding mortality, allowing the populations to increase and become established.

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Acknowledgements

The first person I need to acknowledge before anyone else is Rachel, my wife. Before I started this work there were a few discussions over whether or not I could manage this while working full-time and knowing that our first child was due four months after my planned enrolment. I eventually wore her down and assured her that I could do it, but completely failed to consider what the impact would be on her all those nights I was sat at my desk asking to not be disturbed. To balance work, study and a completely new family life was a tough challenge, and at times I felt as though I was failing at all three but not once did I hear the words “I told you so”. Rachel even joined me on remote beaches while eight months pregnant (no easy feat for those of you familiar with “the steps” at Eastbourne or the long trudge to the beach at Cuckmere!), and then four weeks later with our nine day old son, Fraser, on his very first rock pooling adventure. So, thank you Rachel for being an amazing wife and incredible mother!

Roger Herbert supervised this project and was always on hand for academic guidance, constantly encouraging me to go the extra mile (on top of the 3800 or so driven to collect snails) and do the extra pieces to improve my work and do the results justice. I am genuinely grateful for his assistance, feedback and encouragement.

I should thank friends and family for their understanding; they have seen a lot less of me since January. In the case of my in-laws, they saw a lot more of me and kindly provided me with hearty meals and a place to stay in West Sussex when I was making my field work trips.

At the back of my mind throughout, as always, was my dad. He always told me to work hard, do my best and never quit. His words of encouragement help me when I need it and will always be with me.

1. Climate change and its effects on the distribution of species: a review

1.1 Introduction

The Earth's climate is changing and evidence strongly suggests that although this has occurred naturally several times throughout history, the current period of warming is anthropogenically driven and faster than previously (Walther et al. 2002; Hoegh-Guldberg and Bruno 2010). Incidences of severe weather, droughts, flooding, higher air and sea temperatures, the rate of ice cap loss and rises in sea levels are all increasing as a result of climate change (Liverman 2007). Earth's climate has a strong influence on the distribution of living organisms, and changes to the climate has caused and is predicted to continue to cause, changes in the distribution of some species through range expansions and contractions, as well as extinctions (Hughes 2000; McCarty 2001; Pearson and Dawson 2003; Parmesan 2006; Williams et al. 2008; Chen et al. 2011). Changes to the climate may not impact some species directly if they are able to tolerate the new conditions. However, those unable to survive will need to either adapt physiologically, morphologically or behaviourally, or relocate to an area where conditions are more suitable (Wong and Candolin 2015). Any species unable to adapt or alter their range will face extinction (Holt 1990).

Terrestrial, marine and fresh water habitats are all experiencing reductions in biodiversity and changes to the distribution of species over a wide range of taxa (Sagarin et al. 1999; Parmesan and Yohe 2003; Thuiller et al. 2005; Mora and Sale 2011). The altitude of some mountain plants has increased as temperatures have risen (Klanderud and Birks 2003) and phenological advances in birds has been well documented (Visser and Both 2005; Visser et al. 2006; Charmantier et al. 2008). A range of marine species at all trophic levels from plankton (Hays et al. 2005) to whales (Kovacs and Lydersen 2008) and sharks (Chin et al. 2010) are affected by climate change not only due to changes to sea temperature and ocean chemistry but also their

consequences, such as the distribution of prey species (Kendall et al. 2004) and timings of migrations (Edwards and Richardson 2004). In the Northern hemisphere a general shift to the north has been observed in the geographical distribution of a range of marine species (Perry et al. 2005; Parmesan 2006).

1.1.1 Boundaries and Barriers

At the edge of each species' boundary exists a barrier responsible for restricting their geographic range (Sexton et al. 2009). Even in the marine environment, considered an open system (Caley et al. 1996), many barriers exist limiting a species range. Barriers can be biotic, abiotic, chemical, thermal or physical.

The presence of competitors or predators in neighbouring areas can exclude other species (Connell 1961) while the lack of suitable habitat or food can make the area inhabitable (Paine 1966; Ayre et al. 2009).

Strong tidal flows can be a barrier by restricting or preventing larval supply (Keith et al. 2011) to existing populations requiring external larval input (Gaines and Roughgarden 1985) and new areas yet to be colonised (Gaylord and Gaines 2000). Some predictions indicate that climate change will alter tidal behaviour (Short and Neckles 1999) which could create new or remove existing hydrodynamic barriers. Theoretically, lethal or sub-optimal temperatures can affect the performance of any stage in a species life-cycle, thus limiting reproduction, settlement and recruitment (Hutchins 1947).

1.1.2 Reproduction

Throughout the natural world a range of reproductive strategies exist, with much variation within the same habitat or taxonomic class. Some species reproduce sexually (requiring two individuals), some asexually (requiring one) (Agrawal 2001), and other species have capability for both, with benefits and drawbacks of each. Sexual reproduction increases genetic variability by combining the genes of two individuals; however the trade-off is a lower rate of reproduction because it requires two individuals compared to the one

required in asexual reproduction (Lloyd 1980). Species' reproduction can be one of two strategies: *r*-selection, common in stressful or unstable environments, and K-selection which is generally observed in stable environments (Da Rocha et al. 2015). The characteristics of organisms in each group are displayed in Table 1.1. Each strategy has benefits and limitations. The strategy any particular species displays however, is the result of evolutionary selection and should increase fecundity above the level it would be if the alternative strategy was displayed. For example, humans fall in the K-strategy, taking many years to reach sexual maturity and, generally, producing low numbers of off-spring which require a large amount of parental care, which can be delivered because the number of off-spring produced each time is low. In contrast, a species which reproduces with an r-strategy, common among marine invertebrates (Giangrande et al. 1994) including *Gibbula umbilicalis*, will typically be a small organism that produces a high number of off-spring with little or no parental care.

Characteristics of *r*- and K-selected organisms

r-organisms	K-organisms
short-lived	long-lived
small	large
weak	strong or well-protected
waste a lot of energy	energy efficient
less intelligent	more intelligent
have large litters	have small litters
reproduce at an early age	reproduce at a late age
fast maturation	slow maturation
little care for offspring	much care for offspring
strong sex drive	weak sex drive
small size at birth	large size at birth

Table 1.1: Differences between *r*-organisms and K-organisms (Cunningham et al. 2009).

In the marine environment a range of reproductive strategies are employed; amongst those reproducing sexually, some species give birth to live young and some lay eggs that have been fertilised internally. Following birth/hatching some species receive no care while others might be nurtured for years and even remain in the same group as their parents (Vance 1973; Williams and Lusseau 2006).

Marine invertebrate species utilise a range of reproductive strategies including broadcast spawning, a common trait for the vast majority of benthic invertebrates (Thorson 1950, Crimaldi 2012). These release gametes into the surrounding environment, for external fertilisation in the water column (Thorson 1950). Male and female gamete release is not always simultaneous; Sponges (Porifera) have the ability to reproduce sexually and asexually, but when reproducing sexually only sperm cells are released into the water column which are filtered out by other sponges for internal egg fertilisation. Many marine molluscs reproduce sexually through external fertilisation (littorinids, whelks, chitons, archaogastropods and bivalves). Larger eggs with an increased target area for sperm cells are more likely to be fertilised than smaller eggs (Crean and Marshall 2008).

Changes to the climate can affect reproduction (McCarty 2001) by altering timing and duration of spawning (Both and Visser 2001), which, if no longer synchronous with available food or optimal environmental conditions can result in failed or reduced recruitment (Crick 2004) leading to extinction of the species (Harley et al. 2006) or changes in geographical distribution (Orton 1920).

1.1.3 Climate and Rocky Shore Habitats

Since the first measurements of sea surface temperature (SST) data in the early mid-19th century, mean SSTs have seen an overall increase throughout the English Channel (Southward et al. 1995). It is predicted that SSTs, sea levels and air temperatures will continue to rise as a result of climate change (Jones et al. 1999; Heath et al. 2012; Jevrejeva et al. 2012), which may trigger a range of ecological responses (Hinder et al. 2014). During the 1990s the rate of SST increase was greater than any other decade on record (Mieszkowska et al. 2006) with the mean temperature at the western end of the English Channel increasing by almost 1°C during that decade (Hawkins et al. 2003). In the context of rocky shores along the English Channel, an increase of 1°C over the course of a decade may seem insignificant given that throughout the year, SSTs in the shallow waters can range between 4°C to over 20°C between winter and summer (personal obs.). Moreover, at times of low tide when water becomes trapped in rock pools, temperatures during

winter may fall below 0°C (Mieszkowska et al. 2006) while water temperatures can exceed 30°C in temperate areas under the summer sun (McAllen et al. 1999).

Changes in air temperature and desiccation are among stresses upon rocky shore species with the rise and fall of each tide, exposing organisms to freezing temperatures during winter months and higher temperatures during summer. Yet despite a rise of only 1°C in mean annual SST, changes to rocky shore communities have occurred as some warm water species have shown range extensions with the warming waters, while some (albeit comparatively fewer) cold-water species have shown a retreat (Mieszkowska et al. 2007; Hawkins et al. 2008). Range shifts and extensions could potentially alter the structure of communities and can impact on how they function, especially if the shift involves grazing species (Mieszkowska et al. 2006, Hawkins et al. 2008, 2009).

The use of mean SST data when considering geographic boundaries can be misleading: it is often the case that when temperature restricts a species range, particularly a species moving towards the poles, it is the winter minimum and/or the summer maximum rather than the mean which is critical (Hutchins 1947; Lewis 1986). Winter temperatures can affect the survival of larvae and juveniles which subsequently impacts recruitment (Kendall 1987), while summer temperatures can impact spawning if the required summer temperature does not coincide with gonad maturity (Hall 1964). At the leading edge of a northerly-advancing Lusitanian species range, temperature is an important factor affecting recruitment, either causing mortality during winter (Mieszkowska et al. 2006) or through a reduction in performance or competition with cold-water species (Herbert et al. 2007; 2009).

1.2 Range Extension of *Gibbula umbilicalis*

The marine gastropod *Gibbula umbilicalis* (Da Costa 1778) occurs from North-West Africa (Bode et al. 1986) to Scotland (Kendall and Lewis 1986). The species is present in the North Atlantic off the coasts of Portugal and Spain (Bode et al. 1986; Gaudèncio and Guerra 1986), along the west coast

of Britain (Garwood and Kendall 1985) and the English Channel (Crisp and Southward 1958; Hawkins et al. 2008).

The range of *Gibbula umbilicalis* has extended (Figure 1.1) north along the west coast of Britain and eastwards along the English Channel since around 2000. It has been thought that this is most likely in response to an increase in SST which began in the 1980s (Mieszkowska et al. 2006; Hawkins et al. 2008; Herbert et al. 2009; Keith et al. 2011; Herbert et al. unpublished observations). Previously only found as far east as the Isle of Wight on the English side of the Channel (Crisp and Southward 1958; Kendall and Lewis 1986), the species is now found as far east as Kent in the North Sea (Herbert et al. unpublished). The presence of *Gibbula umbilicalis* along the west coast of the British Isles has been relatively well studied and documented (Williams 1964; Desai 1966; Garwood and Kendall 1985; Kendall and Lewis 1986). However to the best of knowledge no work has been published on the reproduction and recruitment of new populations in south-east England.

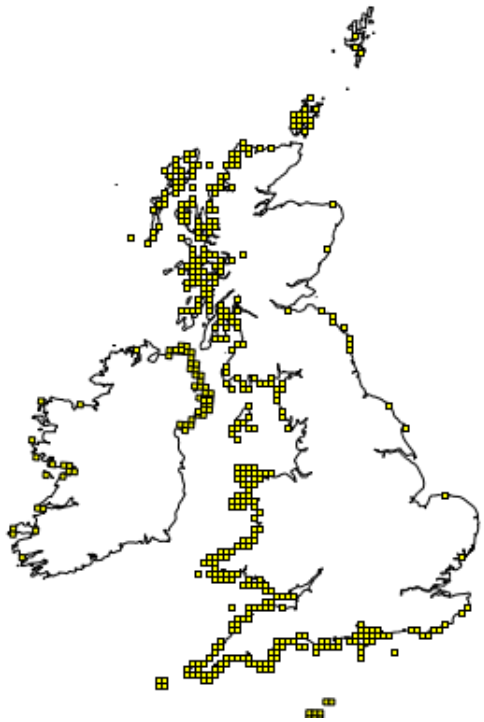


Figure 1.1: Distribution of *Gibbula umbilicalis* around the British Isles. Yellow squares indicate where the species is reported to be present (National Biodiversity Network 2015). The authenticity of some of these records is doubtful, particularly those on the north-east coast of Scotland and England (Herbert – personal communication), Shetland and most of Orkney (Hawkins – personal communication).

Understanding why and how geographical distributions have changed will provide evidence to support future predictions of species distribution as a result of extensions, shifts and contractions, which are expected to increase as climate change continues (Hoegh-Guldberg and Bruno 2010).

Extreme low temperatures have been known to cause the complete loss of entire populations of *Gibbula umbilicalis* on the south coast of Britain (Crisp 1964). Cooler temperatures may not always directly reduce physiological performance, but they can cause changes in behaviour such as reduced feeding by confining animals to rock pools, which in turn will have physiological consequences (Williams 1964). Keith et al. (2011) determined minimum winter temperature tolerances of *Gibbula umbilicalis* at probabilities of 0.1 (7.36°C), 0.5 (7.67°C) and 0.9 (7.98°C). The difference in winter temperature required to increase the probability of *Gibbula umbilicalis* being present from 0.1 to 0.9 is only 0.62°C, and only a 0.01°C increase in the annual mean SST. In laboratory experiments it took between 6 and 24 hours at -5°C to reach 50% mortality with individuals not submerged in water for this duration (Southward 1958). Although air temperatures may sometimes fall to -5°C or below, organisms in most of the intertidal area should never be exposed to the air for 24 hours as tidal periods are less than 12 hours. Further, *Gibbula umbilicalis* is found in the middle to lower shore which is exposed to air for a shorter period at each low tide than organisms further up the shore.

Crisp and Southward (1958) undertook quantitative studies on the distribution of a range of rocky shore species and found *Gibbula umbilicalis* was present only as far east as Bembridge (Isle of Wight) on the English side of the Channel, but further east as far as Calais on the French side. The areas where *Gibbula umbilicalis* was not present in France were formed by long sandy beaches (Crisp and Southward 1958) which are unsuitable for the species. Yet on the English side east of the Isle of Wight, suitable rocky shore habitats are available on the chalk shores along the Sussex coast. This suggested that factors other than lack of suitable habitat was limiting the range. Their research found that *Gibbula umbilicalis* was one of several species which only occurred as far east as the Isle of Wight. Their work also

revealed that some southern species were found only in the west of the English Channel, while northern species were present along the whole Channel but were more abundant in the east, suggesting the west favours southern 'Lusitanian' species, and the east Boreal-Arctic species from the north.

The tidal range in the central part of the English Channel is the smallest in the UK (Pingree and Maddock 1977). A small tidal range reduces the amount of available habitat for intertidal organisms by making each zone narrower. A reduction in habitat will suppress population size and overall propagule numbers, thus reducing the chance of the species successfully reaching new areas. Searches carried out in the 1960s, 80s and 90s revealed that the species was still only present as far east as the IoW on the English side of the Channel (Williams 1964; Kendall and Lewis 1986; Southward et al. 1995). In the 2000s a range extension of the species to the east of the IoW was observed (Hawkins et al. 2009; Herbert et al. unpublished), which coincided with an extension in the north of the species' range (Mieszkowska et al. 2006).

Hiscock et al. (2004) developed a key to predict what the effect of increased air and sea temperatures might be on a range of marine species including *Gibbula umbilicalis*. Following this key on the life history of *Gibbula umbilicalis*, the outcome suggests that, so long as larval dispersal is not interrupted, the range of the species will extend at approximately the same rate that changes to sea and air temperatures occur and that existing populations will become more abundant. Dispersal barriers limiting climate-change driven range extensions was the focus of work by Keith et al. (2011) to understand how climate change could affect biodiversity, as it cannot be assumed that a species range will always be altered in response to climate change. Their work found that the range of *Gibbula umbilicalis* had extended by 141km, some way short of the 243km they had expected and the same "under-performance" was observed for many other species in the study. Of all the species included in their work, *Gibbula umbilicalis* achieved the greatest extension of that expected (58%), while other species managed between nil (*Chthamalus montagui*) and 16% (*Osilinus lineatus*). The failure

of multiple species to reach the maximum of their predicted shift could be attributed to either the influence of factors not considered during design of the model, or a stronger or weaker than anticipated influence of factors that were considered.

Given that temperatures in nearby areas not currently colonised by *Gibbula umbilicalis* are in the tolerant range and suitable habitats do exist, other factors are clearly restricting their range and limiting the extension. One explanation for this could be larval connectivity. This is an important process that can influence the range of a species and meta-population structures (Watson et al. 2010; Selkoe and Toonen 2011). Based on a larval phase lasting at most five days (Fretter and Graham 1994), hydrographic barriers restricting larval dispersal at Portland Bill in Dorset and St. Catherine's Point on the Isle of Wight (Crisp and Southward 1958) may have caused the observed low recruitment (Keith et al. 2011). One similarity between these two sites, which may or may not be significant, is that they are both the most southerly point of the land mass in their regions. To the east of the IoW, the next two notable headlands extending south of the mainland are Selsey Bill and Beachy Head (Figure 2.2). These features may have affected larval transport and recruitment in the same way as Portland Bill and St Catherine's Point. Man-made stone and concrete structures (groynes, sea walls and piers) are potential stepping stones to connect an established population to an un-colonised area between which natural habitats do not exist, so long as the substrate is suitable (Glasby et al. 2007). *Gibbula umbilicalis* has a strong preference for (and greater grazing rate upon) rough surfaces over smooth; most likely because of the protection from predators afforded by crevices and holes (Griffin et al. 2009) making wooden structures less suitable.

1.2.1 Reproduction in *Gibbula umbilicalis*

Gibbula umbilicalis are dioecious trochids although the sex of an individual cannot be determined without dissection and inspection of mature gonads (Underwood 1972). Sexual maturity is thought to occur once the shell width reaches around 8-9mm at the widest point (Williams 1964). Gametogenic development cycles have been linked to sea temperatures (Underwood

1972) which have increased along the English Channel over the last 25 years (Rayner et al. 2003).

When oocytes are growing, a jelly coat forms once the oocytes reach 80-90µm (Garwood and Kendall 1985). As well as increasing the target area for sperm, the jelly coat also increases the amount of time the egg can be suspended in the water column to reduce polyspermy and increase embryo survival and fecundity (Podolsky 2004; Levitan 2005).

Like all trochids, *Gibbula umbilicalis* is a broadcast spawner, releasing gametes into the water for external fertilisation followed by a planktonic larval development stage (Hickman 1992; Bastías 2014).

1.2.2 Spawning

Sea temperatures driving reproduction could lead *Gibbula umbilicalis* to spawn when conditions were favourable and increase reproductive success. If the cue for spawning was less localised, such as phases of the moon as observed in a number of other marine invertebrates (Naylor 2010), spawning could occur at a time when conditions (temperatures) were not optimal for larvae survival and settlement. Partial spawning observed in the UK (Garwood and Kendall 1985) was thought to be caused by sub-optimal environmental conditions (Clare 1986) during the cooler period of the 1960s-1980s (southward et al. 1995). Mediterranean populations are known to spawn multiple times throughout the year (Bode et al. 1986) where sea temperatures are warmer than around the UK, suggesting sea temperature is important. If the cue for spawning was linked to the lunar-phase it would be simultaneous along the coast, as the lunar phase would be the same to the east of the Isle of Wight as to the west at any one time. Conditions required for larval survival (such as sea temperature) may however only be optimal in smaller, localised areas. Oocytes are ejected singly through a gonopore on the right kidney opening (Clare 1986) into the sea to be fertilised, possibly as a response to rough seas (Grange 1976) coinciding with a peak in sea temperature (Gaudèncio and Guerra 1986) as observed in other trochids (Crothers 2001). Previous studies have found that spawning is initially well synchronised between individuals. Following this initial release, however,

spawning continues at a slower rate over a number of weeks (Garwood and Kendall 1985).

1.2.3 Dispersal

Following release of gametes, water movement determines how far and fast they will travel, as until fertilisation has occurred and larvae developed they have no control over their movement. The most critical time for the unfertilised cells is immediately following spawning where the likelihood of male and female gametes meeting is at its greatest because of the high concentration of cells. As time passes the gametes are dispersed and the concentration dilutes. The success of the dispersal stage will have an impact on the population structure and genetic diversity in areas where they eventually settle (Shanks 1983; Underwood and Fairweather 1989; Ayata et al. 2010). The dispersal stage is also the opportunity to advance the range boundary as once settled, individuals will be confined to a small area (Johnson et al. 2001). Tides and currents disperse fertilised gametes and larvae, but the direction and speed of the water can be affected by the shape of the coastline (Gaines and Bertness 1992). The presence of a headland creates an eddy which interrupts the flow of water along the coast, instead of transporting larvae parallel to the coast they are carried away from the shore off the tip of the headland. The larval phase among trochids varies between species, but is generally between 2 and 28 days (Kulikova and Omel'yanenko 2000). For *Gibbula umbilicalis* the length of this stage is not yet known with certainty, but has been suggested as lasting between four and ten days (Lewis 1986) five days (Fretter and Graham 1994) and seven days (Keith et al. 2011). As with sessile and other less-mobile rocky shore species, when larva reach the period in which they can settle, suitable habitat needs to be available (Gaines and Bertness 1992; Johnson et al. 2001). Temperature is important during the dispersal stage; if the water is beyond upper or lower limits for the survival of the larvae there will be a reduction in the number of potential recruits arriving in settlement areas (Hutchins 1947; Rubal et al. 2015).

1.2.4 Settlement

Settlement can be defined as the moment an individual arrives in a new habitat where it will remain indefinitely (Connell 1985). Many stretches of coast around the UK are sandy shores and therefore not suitable for settlement by *Gibbula umbilicalis* larvae. Rocks are needed to provide shelter from predators, something to attach to so they are not swept away, and provide a source of food in the form of algae. Man-made structures (concrete piers, sea walls and groynes) present in what would naturally be an unsuitable area could provide enough habitat for a population to become sufficiently established so that they are able to breed and seed un-colonised areas along the coast. Such structures have been shown to be important in promoting the recovery of other marine gastropod populations that had been in decline (Bray et al. 2012). The connectivity provided by man-made structures is vital for species with a short larval phase if the distance between natural habitats cannot be travelled by the larvae before they perish. Settlement can influence community structure (Wilson 1990) and is a vital link between the planktonic stage and benthic stage of *Gibbula umbilicalis*.

1.2.5 Recruitment

Recruitment can be defined as the "*addition of new individuals to a population or to successive life-cycle stages within populations"* (Caley et al. 1996 p477) which can be through immigration or reproduction. It is essential to differentiate between settlement and recruitment as although organisms may settle initially, post-settlement mortality can occur and limit recruitment (Keough and Downes 1982). Movement of adult *Gibbula umbilicalis* is unlikely to account for new recruitment across sandy beaches because their home range is limited to rocky shores. Post-settlement mortality occurring before the organism has been observed reduces the number of individuals, and thus simply counting new recruits may not always be an accurate way to measure settlement as mortality rates will be unknown.

Juvenile *Gibbula umbilicalis* individuals show a preference for the underside of smooth rocks and cobbles (Kendall and Lewis 1986) while they grow. They are vulnerable to a range of pressures (predation, desiccation, and extreme

temperatures during low tide in summer and winter) which can threaten their initial survival (Gosselin and Chia 1995; Mieszkowska et al. 2013) and cause a complete recruitment failure (Kendall 1987). Recruitment at or near the edge of a geographical range along the south coast of England was observed to be poor and recruitment failure was observed to increase from west to east along the English Channel during the cooler period of the early 1980s (Kendall and Lewis 1986). This could be a result of low density populations, reduction in larval supply, poor habitat, or that minimum or maximum temperature is on the threshold of what the species can tolerate (Kendall and Lewis 1986).

1.3 Conclusion

Changes to the Earth's climate has resulted in changes to the geographic distribution of a range of species, terrestrial and aquatic. *Gibbula umbilicalis* is one example of a species which has responded to increased sea temperatures by exhibiting range advances eastwards along the English Channel since the start of the 21st century. Warmer sea temperatures are considered important for larval survival, supporting post-settlement survival and recruitment in parts of the eastern basin of the English Channel where the species was previously absent. Until now, to the best of our knowledge, no-one has studied reproduction at the new sites to understand the phenology and success of reproduction in comparison to populations that have been established long-term in the western basin of the Channel.

1.4 Aims and Objectives

Two studies undertaken concurrently investigate reproductive development and population structure of *Gibbula umbilicalis* at four different locations along the south coast of the United Kingdom; two at pre-range extension areas to the west of the Isle of Wight and two in post-range extension areas to the east. Chapter 3 aims to understand the rate and synchronicity of gonad and oocyte development at different locations and Chapter 4 investigates population structures, recruitment and density as well as whether any of the new populations can yet be considered established and no longer "new".

1.4.1 Research Questions

1.4.1.1 Reproduction

Is gonad development synchronous at the different sites?

This is important to understand as it will show whether breeding is occurring at the same time irrespective of location and/or sea temperature.

If gonad development is not synchronous, are development rates the same in different populations?

It may be that some populations develop at a faster or slower rate than others, which may influence the success of breeding.

Is there a link between gonad development and sea surface temperature?

An answer to this question may support the theory that sea temperature is important for breeding either as a cue for spawning and to increase recruitment.

1.4.1.2 Population Structure and Growth

Is there evidence of recent recruitment at all locations?

Evidence of recent recruitment will demonstrate that previous recruitment was not a coincidental event in new locations.

Are there differences in population structure between sites?

Differences in recruitment can be detected by looking at the size of individuals within a population and evidence of juveniles.

Does population density influence the size of individuals?

It is common for individuals to be larger where their density if low (perhaps as a result of reduced intra-specific competition), however, any populations where this does not occur could be an indicator of other pressures.

Can some of the “new” populations to east of the Isle of Wight be considered established yet?

Population densities similar to older sites and evidence of continuing recruitment will suggest that populations in the extended range area are established.

2. Environment and Study Sites

2.1 Study Sites

Four sites (Figure 2.2) along the south coast of England were chosen where *Gibbula umbilicalis* is known to exist. Two sites to the west of the Isle of Wight (Lyme Regis and Osmington Mills) which are pre-range extension sites and two sites to the east (Cuckmere Haven and Eastbourne), which are new sites resulting from the range extension.

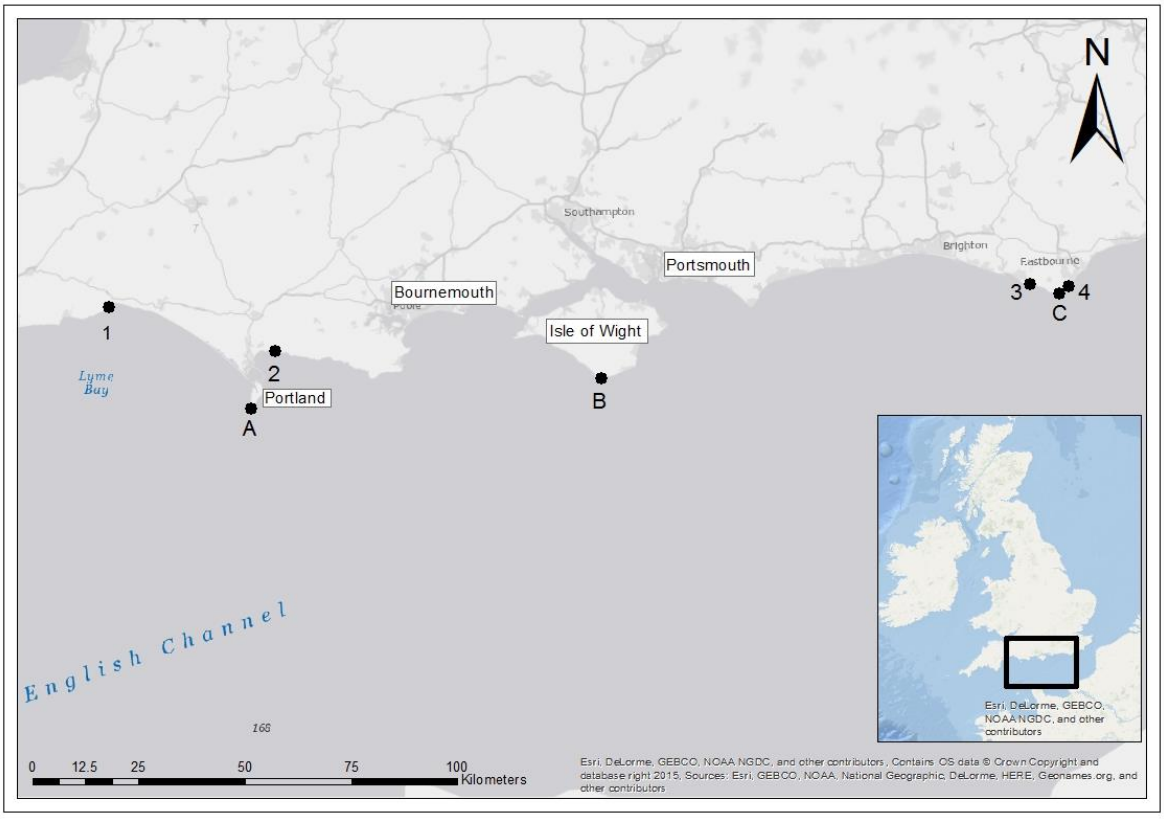


Figure 2.2: Study site location map. Study Sites: 1-Lyme Regis (50º 43.476'N, 2º 55.709' W), 2-Osmington (50º 38.027'N, 2º22.576'W), 3-Cuckmere (50º 45.513'N, 0º 8.777'E), 4-Eastbourne (50º 44.929'N, 0º 16.152'E). Headlands: A-Portland Bill, B-St. Catherine's Point (Isle of Wight), C-Beachy Head.

2.1.1 Lyme Regis

Lyme Regis is half way between Exmouth and Portland in Lyme Bay, Dorset, and has a south-west facing aspect. Lyme Regis is a small town popular with tourists during the summer, many of whom choose to visit the shore which is

easily accessible and often busy with people rock pooling and fossil hunting. There is a small stream (River Lym) which discharges fresh water into the sea 250m west of the survey area. The shore where searches were carried out (50º 43.476'N, 2º 55.709'W) consists of flat rocky ledges with some loose cobbles present as well as a small sandy beach at the upper part of the intertidal area. Nearby there is a harbour surrounded by a concrete and stone sea wall (the Cobb) and a high concrete sea wall at the base of vertical cliffs is present to the east of the town to prevent coastal erosion which occurs frequently in the area. The gradient of the shore is shallow and during a spring tide when there is a vertical difference of 3.80m between high and low water, the sea retreats approximately 250 metres to expose a rock platform (Top left (Figure 2.3). The level of exposure the shore is subjected to along with the morphology does not allow algae to completely dominate, however it is abundant in the upper zones and in a sheltered area next to an old sea wall. The rock is a Blue Lias Jurassic limestone, with a worn surface on top but is rough on vertical faces. Loose rocks and cobbles made of limestone and clay are present but not abundant.

2.1.2 Osmington Mills

Osmington Mills is 6km north-east across the bay from Weymouth and the shore faces approximately south-west and is sheltered by Portland from storms originating in this direction. The shore where searches were carried out and from which snail samples were taken is made up of a combination of large boulders (sandstone), cobbles (sandstone and limestone) and wave cut platforms. A small river discharges fresh water from the base of the cliff onto the beach approximately 50 metres from the survey area. The shore is not easily accessible as the route down is precarious and not well maintained, which may deter some visitors. The beach is difficult to walk over because of the loose nature of the substrate. The cliffs here contain Jurassic sandstone, clay and limestone with large boulders present.

The survey area (50º 38.027'N, 2º22.576'W) experiences a 1.8m tidal range during spring tides with an approximately 80m retreat of the sea during low tide. Ledges in the intertidal zone are exposed at low tide along with large boulders and cobbles.

2.1.3 Cuckmere Haven

Cuckmere Haven is 4km east of Seaford and is where the Cuckmere River and Estuary enters the sea. Cobble beaches are present either side of the river mouth, with the area to the west having three wooden structures/groynes which extend south into the sea for approximately 50 metres. The area is popular with visitors however these mostly visit the beach area to the east of the river as this is the easiest part to access from the visitors centre. Searches were carried out in the area beneath the old Lifeguard Cottages (50º 45.513'N, 0º 8.777'E) which, at low tide comprises of chalk platforms and cobble banks Bottom left (Figure 2.5). Brown alga are abundant on the chalk platform, but becomes rare on the cobbled area, other than on larger boulders. At high tide the sea completely submerges some stretches of the shore all the way up to the concrete sea wall beneath the cottages.

2.1.4 Eastbourne

Originally Hastings was chosen as the most easterly site. On a visit prior to the first survey the area intended for the study was however, found to be closed off due to a cliff fall and Eastbourne was identified as a suitable substitute. The shore at Eastbourne (known as Hollywell Ledge) is approximately 10km east of Cuckmere Haven with a headland (Beachy Head) between the two sites. The intertidal area comprises smooth sandstone (Upper Greensand) on the upper shore and rough sandstone ledges further down. Above the strand-line the beach is made up of large cobbles and boulders, of which a few are also found scattered in the intertidal zone. The shore is moderately easy to access via a steep set of steps down the cliff. Once on the shore it is, however, slippery underfoot due to the algae-covered smooth rocks; the area was not observed to be busy (no more than 20 people were ever seen in the area during visits despite some of them being undertaken in the middle of a warm sunny day). The search area (50º 44.929'N, 0º 16.152'E) is smooth sandstone with some rock pools and large boulders. The smaller loose rocks preferred by juvenile *Gibbula umbilicalis* are less common here than at other sites.

Top left (Figure 2.3): Lyme Regis survey area viewed from the sea wall.

Top right (Figure 2.4): Osmington Mills survey area.

Bottom left (Figure 2.5): Cuckmere Haven survey area looking east.

Bottom right (Figure

2.2 Sea Temperature

Since 1980 the Northern hemisphere has been warmer than any other period in the last 2000 years (Philippart et al. 2011). Since 1980 mean annual sea temperatures in the English Channel have risen (Figure 2.7) (Rayner et al. 2003; Met Office 2015a).

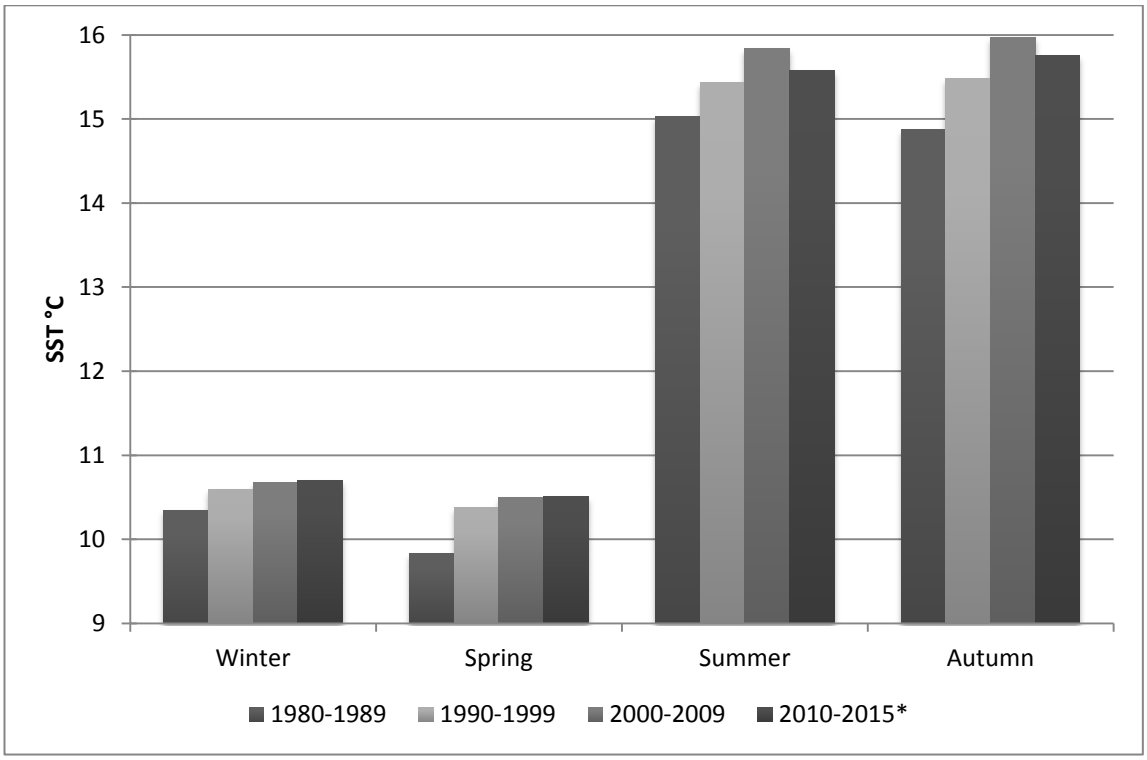


Figure 2.7: Mean sea Surface Temperatures for cell grid reference 50.5N, 1.5W. *Autumn data represents 2010 – 2014 as 2015 data has not been published yet. Chart compiled based on HadISST data from the Met Office (2015a) website (Rayner et al. 2003). Winter = December to February, Spring = March to May, Summer = June to August, Autumn = September to November.

Between 1971 and 2011 mean annual sea temperatures at Weymouth and Eastbourne fluctuated, with an overall increasing trend (Figure 2.8) (Cefas 2015).

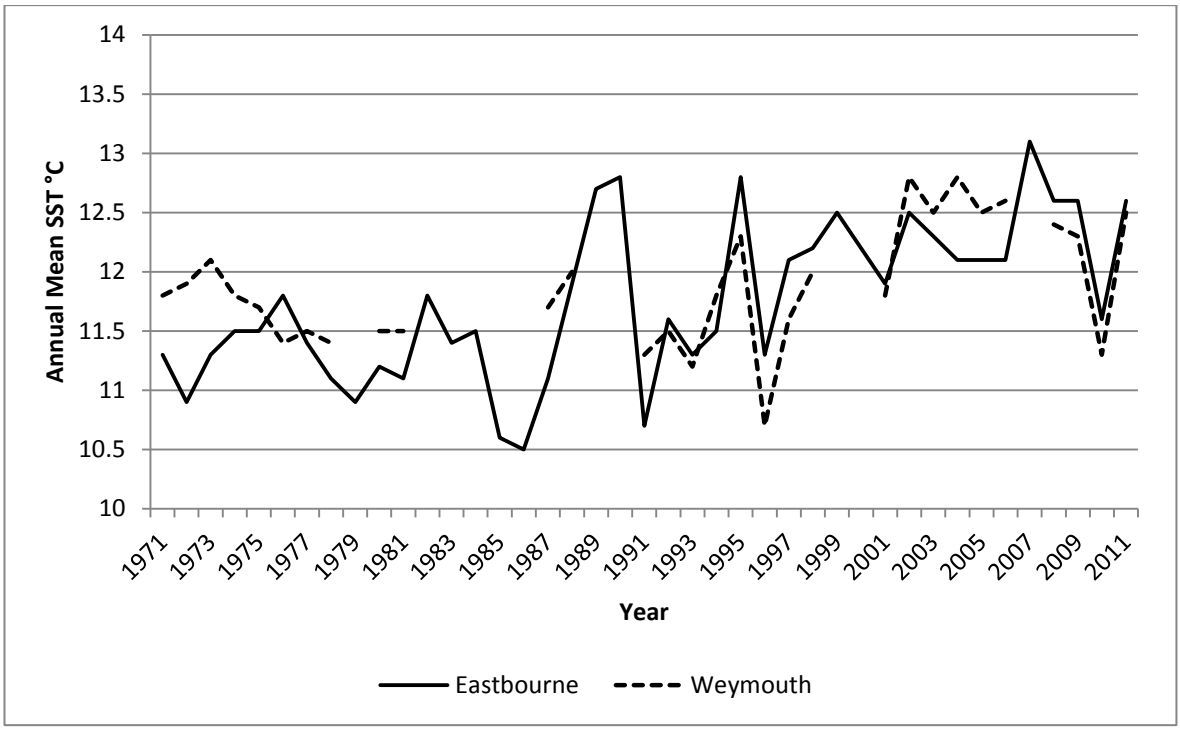


Figure 2.8: Mean annual sea temperatures for Weymouth and Eastbourne 1971-2011.

Sea temperature data for two cells in the Channel (50°N, 2.5°W in the western basin and 50°N, 0.5°E in the eastern basin) show that between 2011 and 2015 mean spring and summer SSTs fluctuated each year (Figure 2.9). The greatest anomalies below the mean spring temperature for the five year period occurred in 2013 (difference of 1.24°C in the western cell, 1.68°C eastern cell). During 2013 the lowest mean monthly temperatures for the period 2011-2015 occurred in April in the western cell (8.9°C) and March in the east (7.4°C).

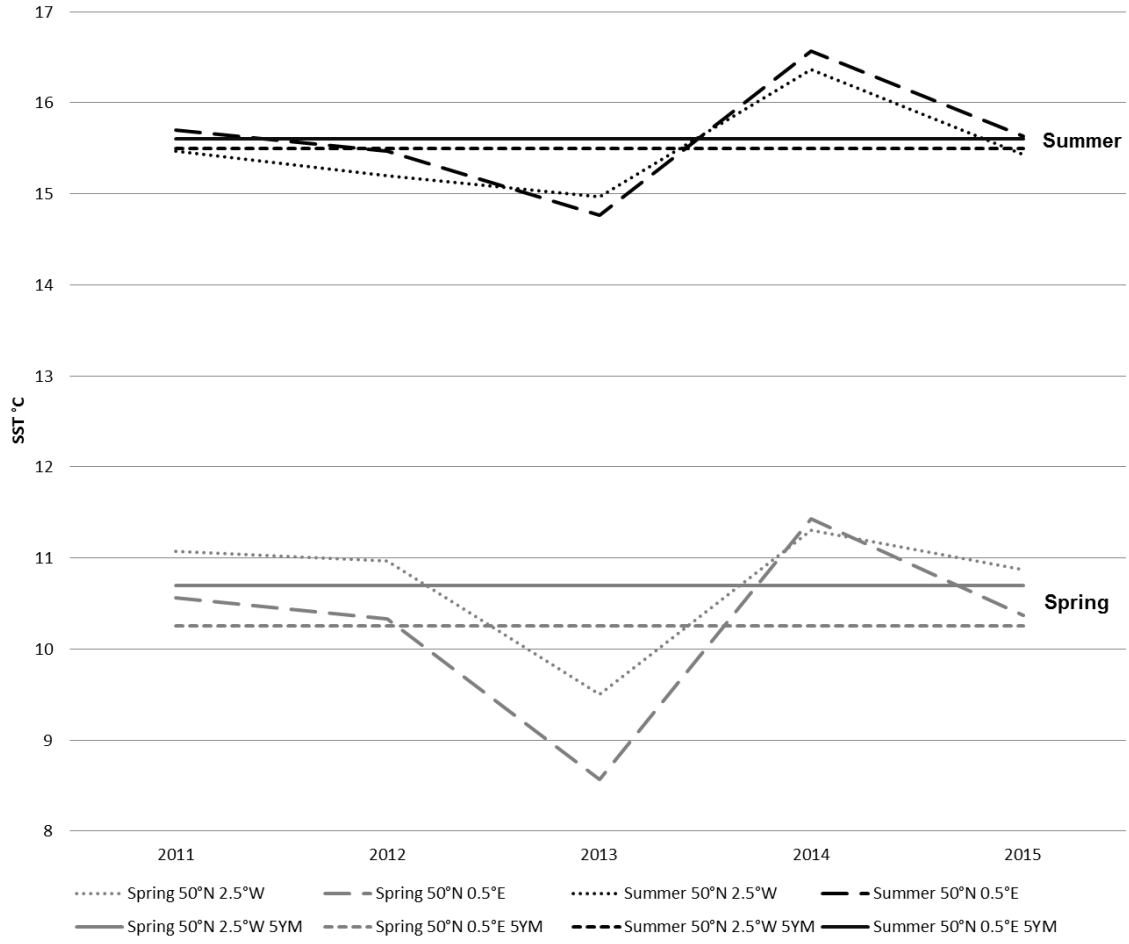


Figure 2.9: Spring and summer mean SSTs for areas in the western and eastern basin of the Channel since 2011. Spring: March to May. Summer: June to August. 5YM=5-year mean.

Sea surface temperature (SST) data were collected in the study areas to establish if there is a link between sea temperature, reproductive development and spawning. SSTs were recorded on the day of each collection using data obtained from the sensor closest to each field site (Table 2.2) published on the Channel Coast Observatory website (2015).

Site	Sensor location	Sensor location relative to site
Lyme Regis	50.69339 -2.74997	13km ESE
Osmington	50.62291 -2.41485	3km WSW
Cuckmere	50.76633 0.07540	5km W
Eastbourne	50.78339 0.41744	11km ENE

Table 2.2: Sea temperature sensor locations.

According to historical SST data (Cefas 2015) the minimum temperatures experienced in Weymouth and Eastbourne since the 1990s were not as low as they were in previous decades, especially cold winters of the early 1960s (Crisp 1964). In the western basin of the Channel Weymouth has only fallen below 6°C during three winters since 1990, while in the eastern basin, temperatures have frequently fallen below this level, and as low as 3°C at Eastbourne. Crucially, during this period, winter sea temperatures in Eastbourne have only occasionally fallen as low as 7°C, which is the lower end of the tolerable range for survival of *Gibbula umbilicalis* (Keith et al. 2011). These instances may have occurred sufficiently frequently to limit juvenile winter mortality.

Historical air temperatures at Eastbourne were reviewed as far back as 1990 using Met Office (2015b) data, but only monthly means were available so it is not possible to know what the coldest temperatures recorded were. The coldest month on record during that time was December 2010 with a mean air temperature of -0.5°C (Met Office 2015b). Data containing the lowest temperature recorded in each month as far back as January 2012 are available from an amateur weather station in Sovereign Harbour, Eastbourne. In February 2012 a low temperature of -5.7°C was recorded, at no other time as far back as January 2012 did the temperature fall below -5°C according to the data from this sensor (BRXNET.org 2015). The lowest temperature recorded at each site was during March (8.5°C Lyme Regis and 8°C at all other locations) with the warmest occurring during August (Lyme Regis and Osmington 18°C, Cuckmere 18.5°C and Eastbourne 19.1°C). Sites in the eastern basin had a mean temperature that was 0.25°C lower than the western basin during March and April. From May onwards the eastern basin was warmer than the west by between 0.6°C and 0.8°C. The largest difference between the coolest and warmest site during the same

month was 1.1°C which was between Lyme Regis (17°C) and Cuckmere (18.1°C) in July, and Lyme Regis (18°C) and Eastbourne (19.1°C) during August. During the cooler months Lyme Regis, the most westerly site, had the warmest sea temperature, but during the warmest month it was Eastbourne (the most easterly site) which recorded the highest temperature while Lyme Regis had the lowest temperature. Temperatures recorded are presented graphically (Figure 2.10) as well as Figure 2.11 which also displays the monthly means temperatures for 2011-2015 in the western and eastern Channel.

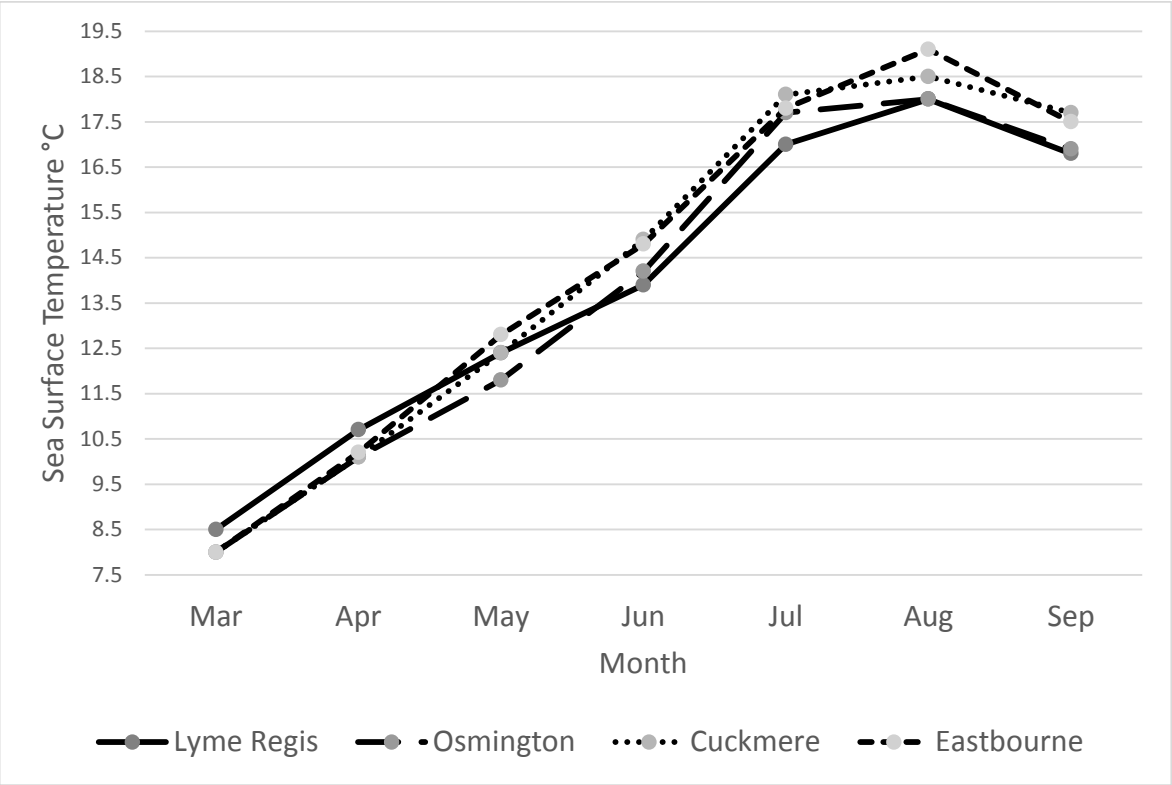


Figure 2.10: Sea temperature data collected from each site on the day of each field visit in 2015.

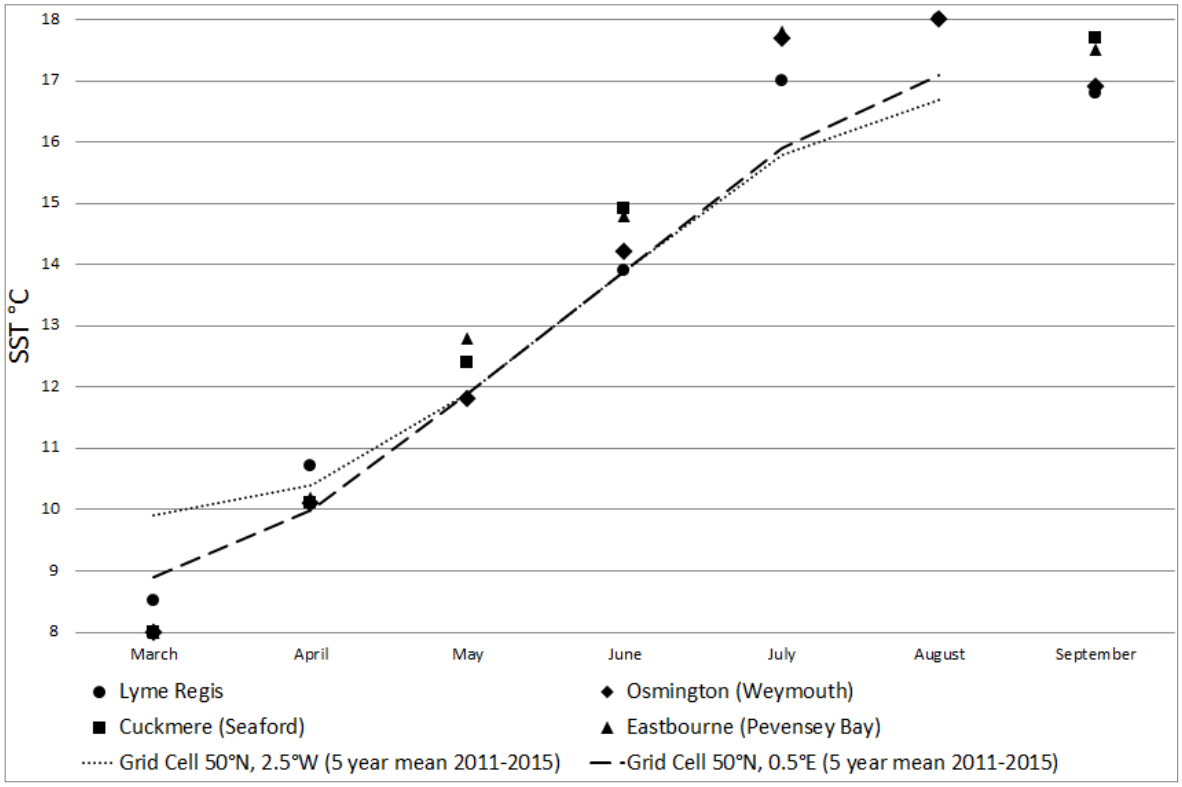


Figure 2.11: 2015 monthly mean SSTs for four locations in the Channel with monthly means for the period 2011-2015 shown.

3. Reproductive Development

3.1 Introduction

Sexual maturity in British populations of *Gibbula umbilicalis* is thought to occur when individuals are approximately 18 months old with a shell width of 8-9mm (Williams 1964). Sexually mature females produce oocytes which when fully mature have a diameter up to 180µm (Garwood and Kendall 1985). Spawning and settlement in *Gibbula umbilicalis* occurs annually in British populations (Williams 1964; Underwood 1972). This contrasts with populations in areas with warmer sea temperatures off the coast of Portugal and northern Spain where multiple spawning events occur throughout the year (Bode et al. 1986; Gaudèncio and Guerra 1986).

Synchronisation of male and female gamete release is essential for reproduction to be successful. In *Gibbula umbilicalis* a large number of oocytes are initially released when spawning commences, with the remainder released over the following weeks (Underwood 1972; Garwood and Kendall 1985). A prolonged spawning period has advantages over a shorter, single event by offering a form of protection against freak environmental events and a mismatch in synchronisation of spawning between males and females. Synchronisation between different populations is not important as unfertilised gametes are not likely to survive for the time it may take to reach another spawning population. It is imperative, however, that both sexes in each population are ready to spawn at a time that will favour survival of the larvae and settling juveniles.

New populations of *Gibbula umbilicalis* (observed since approximately 2000) to the east of the Isle of Wight (IoW) on the English side of the Channel are thought to be a result of an increase in sea temperatures (Hawkins et al. 2008; Herbert et al. 2009), which during the 1990s were greater than any other previous period on record (Houghton et al. 2001).

The aims of this chapter are to determine whether reproduction is synchronised among different populations and whether it is linked with temperature.

3.2 Methods

Between March and September 2015, reproductive development was studied at four sites. Two sites west of the Isle of Wight (Lyme Regis and Osmington Mills) have had long-established populations (Crisp and Southward 1958) whereas the two sites east of the Isle of Wight (Cuckmere and Eastbourne) have only colonised since 2000 (Herbert pers. comms.).

Female gonad development was investigated in two ways:

(i) Visual examination of the gonad to determine the stage of reproduction based on appearance, colour and size;
(ii) Measurement of oocyte diameter over the summer months as they mature.

Spawning can be detected by observing changes in the exterior appearance of the gonad, as well as a decrease in the density of oocytes inside.

Samples were collected every four weeks. Twenty-five adults from each of the four locations were stored in sea water for between 24 and 48 hours before being processed in the laboratory. Individuals were selected at random and checked to ensure they were above 10mm, when they become sexually mature (Williams 1964). The animals were not fed following collection to allow their digestive system to empty, making the dissections easier. It was not possible to keep the animals at the same temperature as the sea during the period between collection and the laboratory work. They were stored in a naturally lit room without heating to allow the temperature to fluctuate between day and night, mimicking the temperature outside. Fluctuations in temperature are a daily occurrence for this species as it lives in the intertidal zone. All individuals removed from the shore were still alive when they were delivered to the laboratory.

Each individual had the shell maximum basal diameter (MBD) measured with callipers to the nearest 0.1mm in the laboratory before being assigned a number and placed in a labelled 25ml plastic Sterylin® tube. Once all 25 individuals had been measured they were individually cracked open using mole-grips. The best result was achieved by placing the animal upright in the mole-grips so that the jaws compressed vertically from top to bottom. The shells are strong and a considerable amount of force is required; using this method results in minimal damage to the internal tissue. Once the shell had been cracked the animal was returned to the Sterylin® tube and Formalin (4% buffered $MgCl_2$) added and lid replaced. Cracking the shell allows the formalin to penetrate more of the tissue than if the animal was simply dropped in un-fractured because it would close its water-tight operculum. This could result in some internal tissue not being preserved sufficiently. The gonads are located in the top part of the shell so it was vital that the preservative was able to reach this region.

When ready for dissection the animals were removed from their Sterylin® tube, the shell separated from the internal soft tissue and the sex determined from visual examination of the gonad. Initially it was difficult to distinguish between male and females because they were similar colours when the gonads were not mature, therefore each specimen was viewed under the microscope to look for the presence of oocytes. The presence or absence of eggs determined whether the individual was female or male.

Dissection of the animals was completed by holding the body of the animal with tweezers and slicing away a portion of ovary. The ovary tissue was then placed onto a clean microscope slide and sliced further to release oocytes so that they lay level on the glass slide. Cavity slides contained the oocytes in sea water to prevent desiccation and shrinkage while being viewed.

The gonad tissue was viewed under a microscope (Keyence VHX-5000 digital microscope fitted with a 20-200x zoom lens) using a white, high-power LED light (5700k) to allow the tissue to be observed with natural colouration. The microscope was connected to a PC for viewing images on a screen. The accompanying software has an array of options for improving and adjusting

the image as well as tools to make measurements of the tissue under the microscope.

Oocyte diameters were measured on screen (Figure 3.12) and labelled with the survey number and tube number for later cross-referencing with the MBD values. To minimise issues with the data quality that would occur if oocytes of different shapes were measured for comparison, oocytes that were as round as possible were measured, but were otherwise selected at random. In cases where oocytes were surrounded by a jelly coat (Underwood 1972; Garwood and Kendall 1985), this jelly coat was not measured.

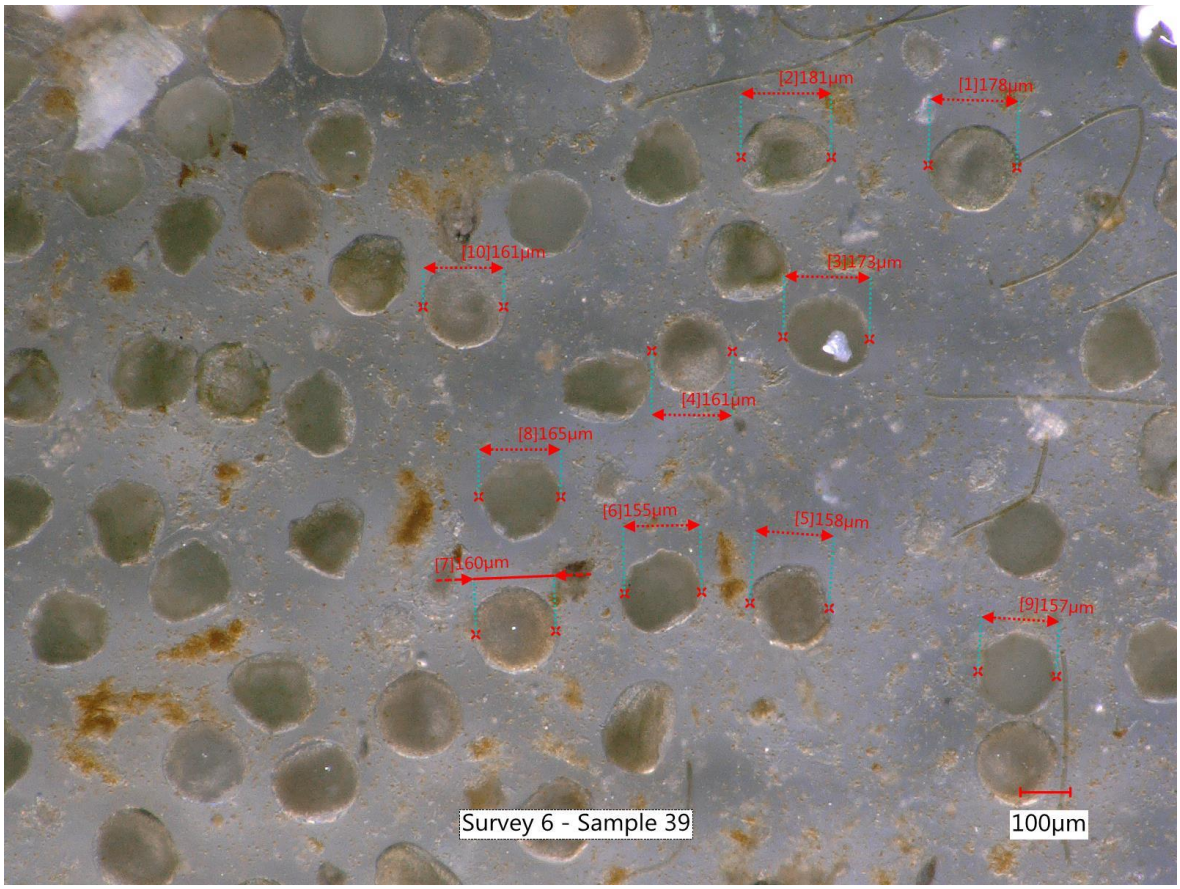


Figure 3.12: Digitally measured oocyte diameters from a sample collected during August 2015 from Osmington.

The stage of female gonad development was assessed using an adapted version of the index devised by Williams (1964) which was based on an existing staging index for a similar species *Phorcus lineatus* (Desai 1959).

Stage	Description
Stage I	Brown in appearance, inactive/spent – difficult to distinguish sex of individual.
Stage II	Gonad is light green and contains large number of small oocytes.
Stage III	Gonad green, oocytes have grown and represent honeycomb in appearance.
Stage IV	Gonad green, oocytes now grey/green in appearance and the honeycomb resemblance is very obvious.
Stage V	Similar to stage IV, but oocytes are noticeably larger and mostly grey/green and ovary appears very swollen.
Stage VI	The ovary is partially spent but still contains large oocytes. The external appearance of gonad tissue appears wrinkled. Green colouration of ovary is maintained and oocyte size remains large. Small oocytes beginning to develop for the next cycle may be present.

Table 3.3: Female gonad development staging index adapted from Williams (1964).

The gonad development stage index shows how individuals and populations are developing reproductively over time and can indicate whether development is synchronised between individuals within a population, or between different populations. Although it contains five stages of development, none of those are relevant if the animal has partially spawned. Stage V relates to animals capable of spawning and Stage I is for animals in a spent state. To allow differentiation between animals capable of spawning and those which have partially spawned, a sixth stage (VI) was created and given the definition below.

Stage VI	Green colouration of ovary is maintained and oocyte size remains large. Ovary contains fewer oocytes than stage V and as a result the ovary tissue has a wrinkly appearance.

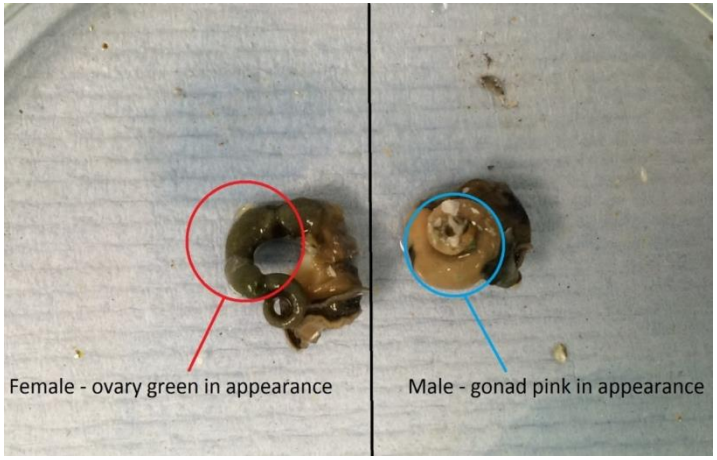
A spawning stage index (Table 3.4) was created by Williams (1964) consisting of three stages makes the link between the final and first stage of the development index. The first spawning stage matches development Stage V and the third spawning stage matches development stage I. Spawning Stage II relates to partially-spawned animals, and consideration could be given to merging the two indexes (Development and Spawning) together so that one index completes a full reproduction cycle, as in this study (Table 3.3). The addition of oocyte sizes to the index may make the staging process more objective.

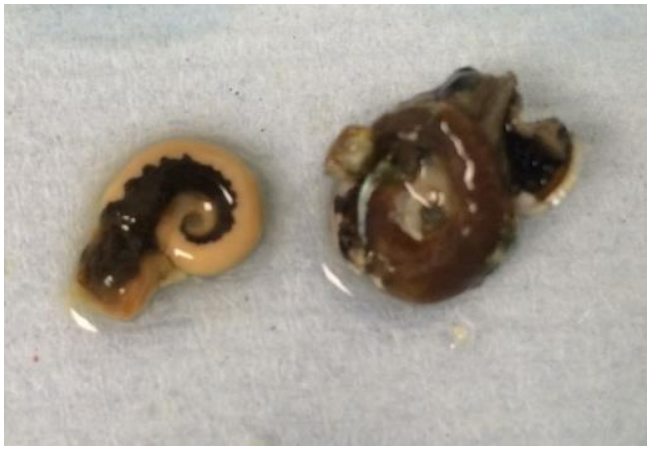
Stage	Description
Stage I	Similar to development stage V. Capable of spawning, ovary large and tightly packed with large oocytes.
Stage II	Half-spent. Ovary has reduced in size but still contains many large oocytes.
Stage III	Similar to development stage I. Ovary is brown in appearance and an empty, loose sac possibly containing a small number of oocytes.

Table 3.4: Female spawning stage index. *Source: Adapted from Williams 1964.*

3.3 Results

The gonads are located at the posterior end of the body with the digestive gland running alongside part of the gonad. Once gonads had begun to mature in April the differences in appearance were much more apparent with females presenting as olive green and males creamy-pink (Figure 3.13), although some males were infested with a suspected parasitic trematode as observed by previous researchers (Williams 1964; Underwood 1972) which altered their appearance from creamy-pink to a reddish-brown (Figure 3.14). In one instance the appearance was bright orange and the orange trematodes were visible (Figure 3.15). As females were the focus of this study, records were not kept of the sites and months that infested males were observed. The oocytes appeared cream/white with a smooth surface texture during early surveys (Figure 3.16) turning grey from July. The oocytes were spherical when released from the ovary, unlike when contained inside, tightly packed causing irregularity in their form.





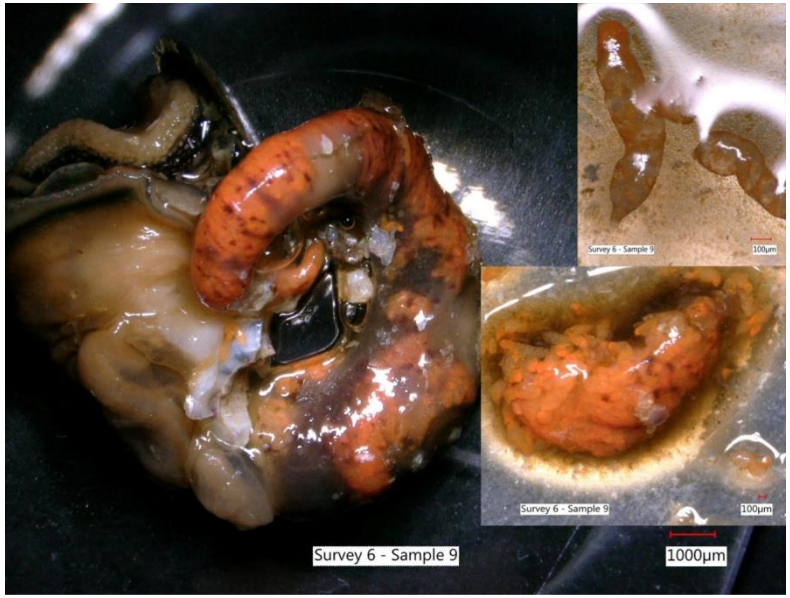


Figure 3.13: Top left - External appearance of gonads in mature individuals. Figure 3.14: Top right - Comparison of a healthy male (left) and infested male (right). Figure 3.15: Bottom left - heavily infested male. Figure 3.16: Bottom right - Oocytes cream/white in colour (Lyme Regis, March).

3.3.1 Gonad Development

The gonad staging results are presented in Figure 3.17 with corresponding monthly SSTs for each site. Snails at Osmington were already at Stage III when surveys began in March and remained at this stage until June. Lyme Regis, Cuckmere and Eastbourne were all at Stage II in March (see Figure 3.18). By April Lyme Regis and Cuckmere had progressed to Stage III and the ovaries contained high numbers of large white oocytes (Figure 3.19) but Eastbourne, the most easterly site, remained at Stage II for another month. All populations remained on Stage III for May and June. Gonad stages were fully synchronised among all individuals at all sites each month. The transition from Stage III to IV occurred during the same four week period in all populations between 13th June and 11th July. All populations were at Stage IV during July but by August only those at Lyme Regis and Osmington, the western sites, had progressed to Stage V (Figure 3.20). By September populations at Lyme Regis and Osmington were at Stage VI; the ovaries were no longer tightly packed as spawning had begun (Figure 3.21). However, although animals at Cuckmere and Eastbourne had progressed to Stage V, ovaries remained large and densely packed indicating spawning had not yet begun.

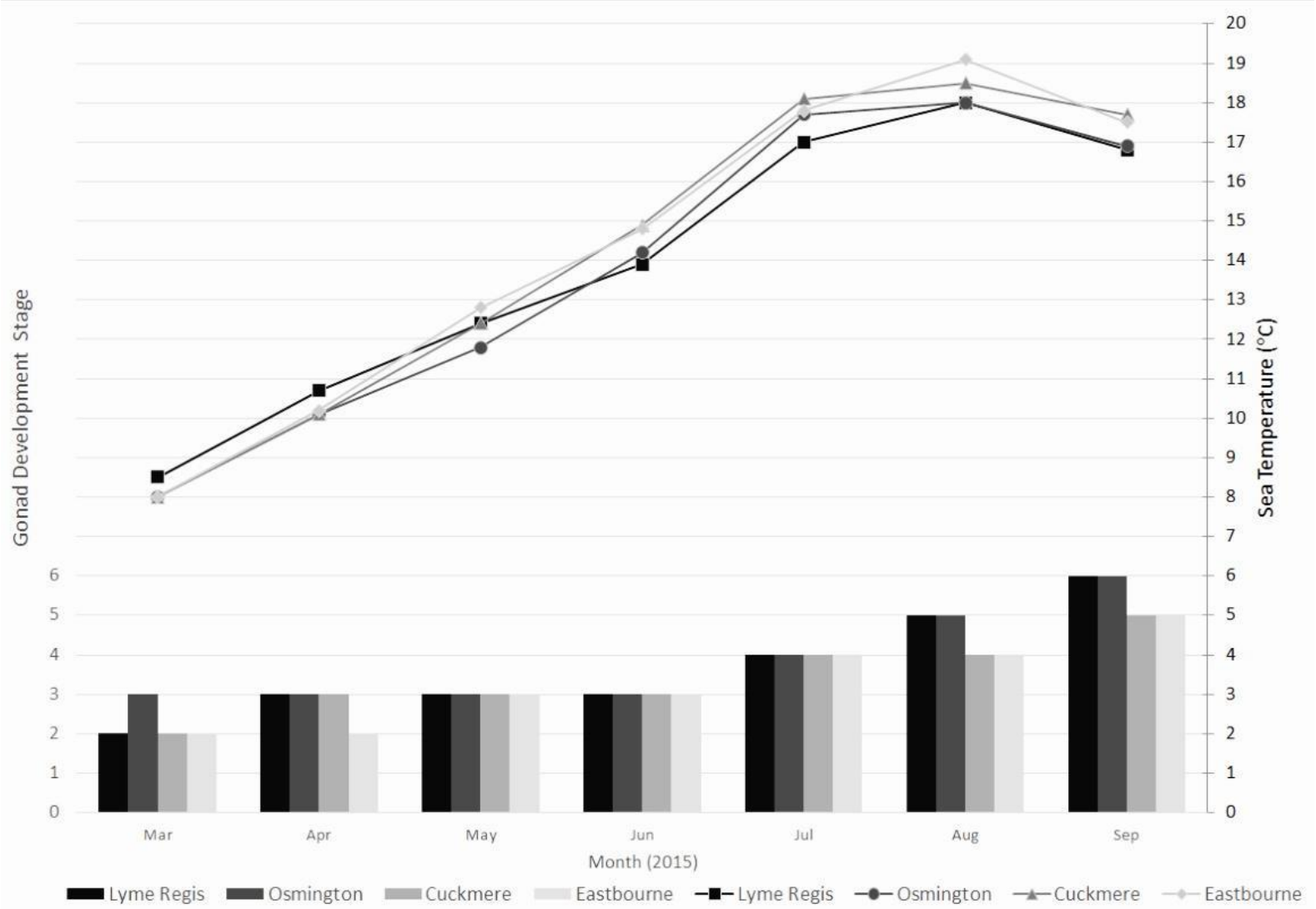


Figure 3.17: Gonad development results for Lyme Regis, Osmington, Cuckmere and Eastbourne for 2015 using the Gonad Staging Index based on Williams (1964) (Table 3.3). Sea temperatures measured on the day of each survey are displayed above.

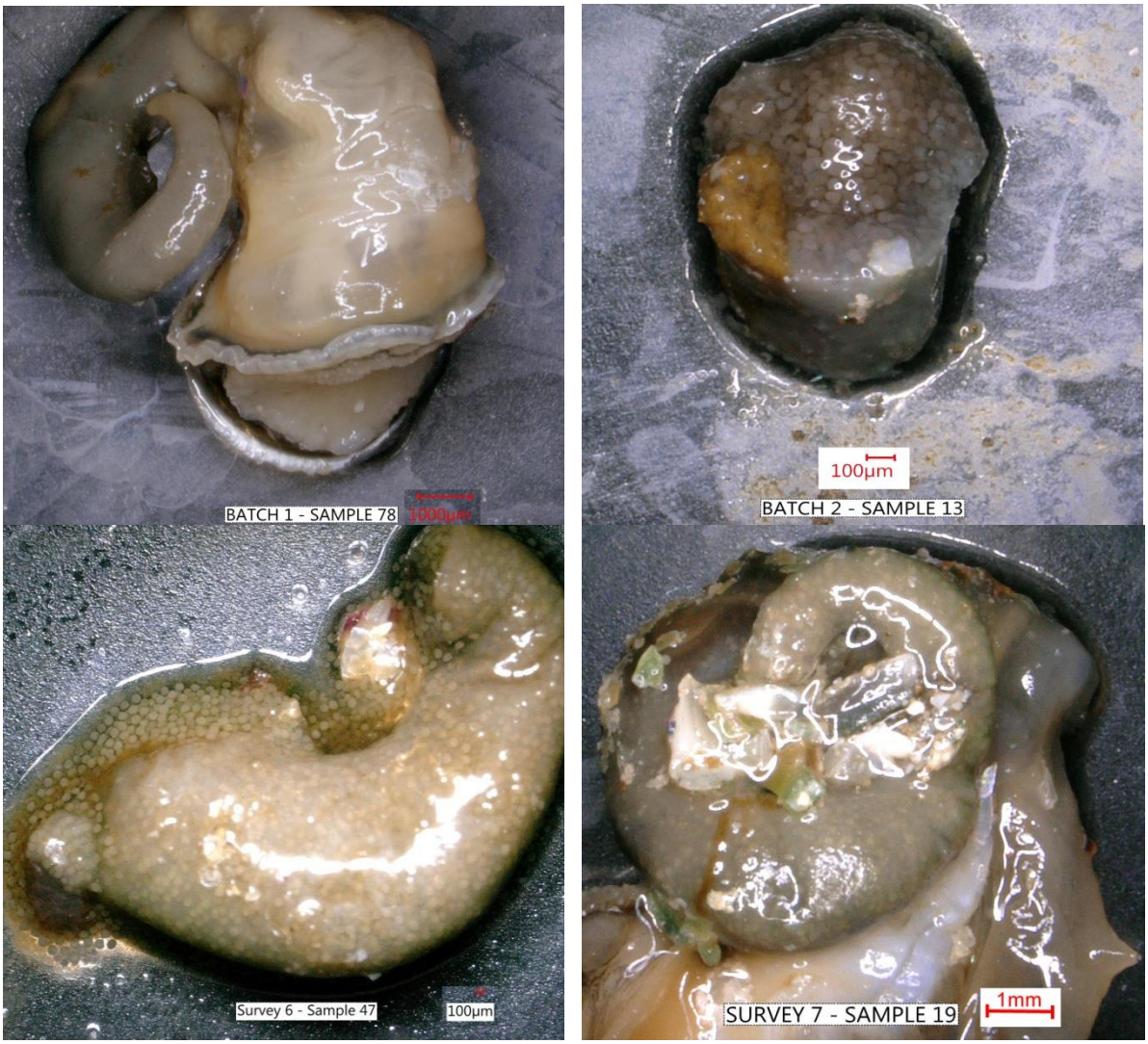


Figure 3.18 top left: Female at reproductive stage II (Cuckmere, March). Figure 3.19 top right: Portion of stage III ovary (April, Lyme Regis). Figure 3.20 bottom left: Portion of swollen stage V ovary (August, Osmington). Figure 3.21 bottom right: Example of ovary at development stage VI (Lyme Regis, September).

3.3.2 Oocyte Growth

Oocyte growth was well synchronised among each population during each month. Populations obtained in September that had mature oocytes and were at the same stage (V) of gonad development were subjected to a 2-tailed Pearsons bivariate correlation test (output presented in Appendix A). This showed a weak positive correlation between oocyte size and shell MBD (Figure 3.22) which was not statistically significant (n=32, r=0.143, p=0.436). On this basis, animal size was not considered to be relevant during analysis of gonad development and oocyte growth which is consistent with Garwood and Kendall (1985).

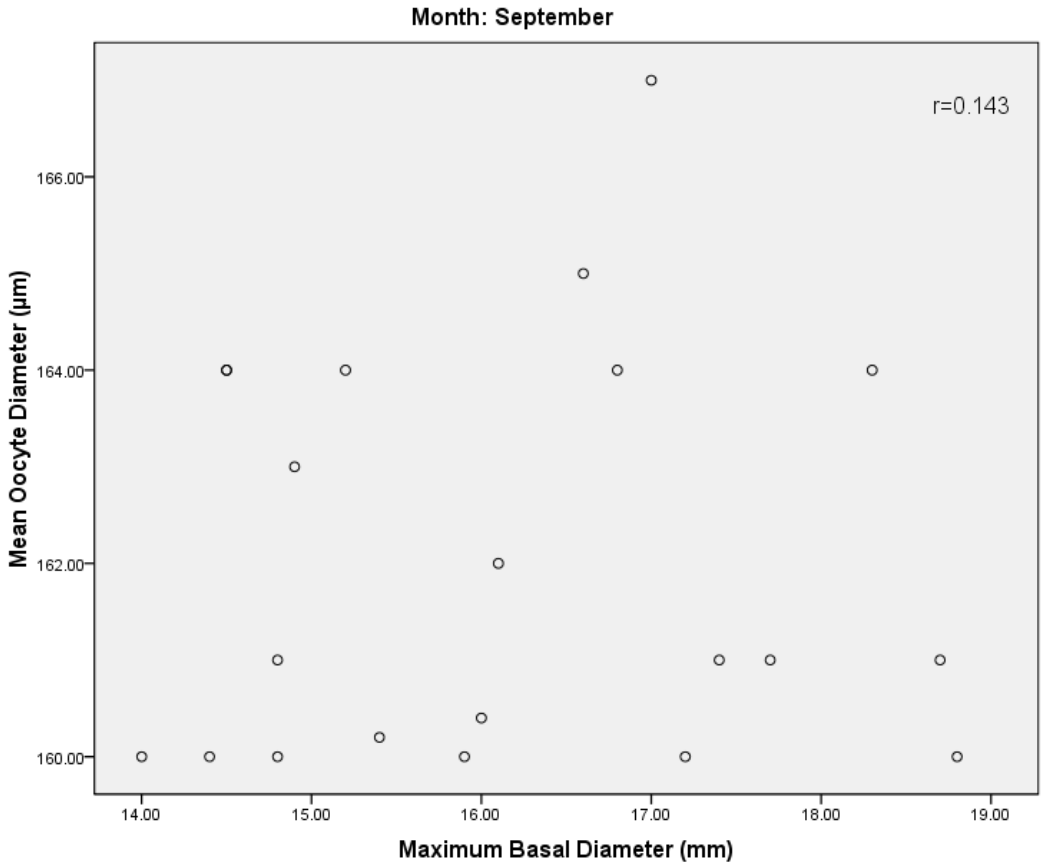


Figure 3.22: Relationship between shell size (MBD) and oocyte size.

Full oocyte measurement results for the study are presented on the following page in Figure 3.23.

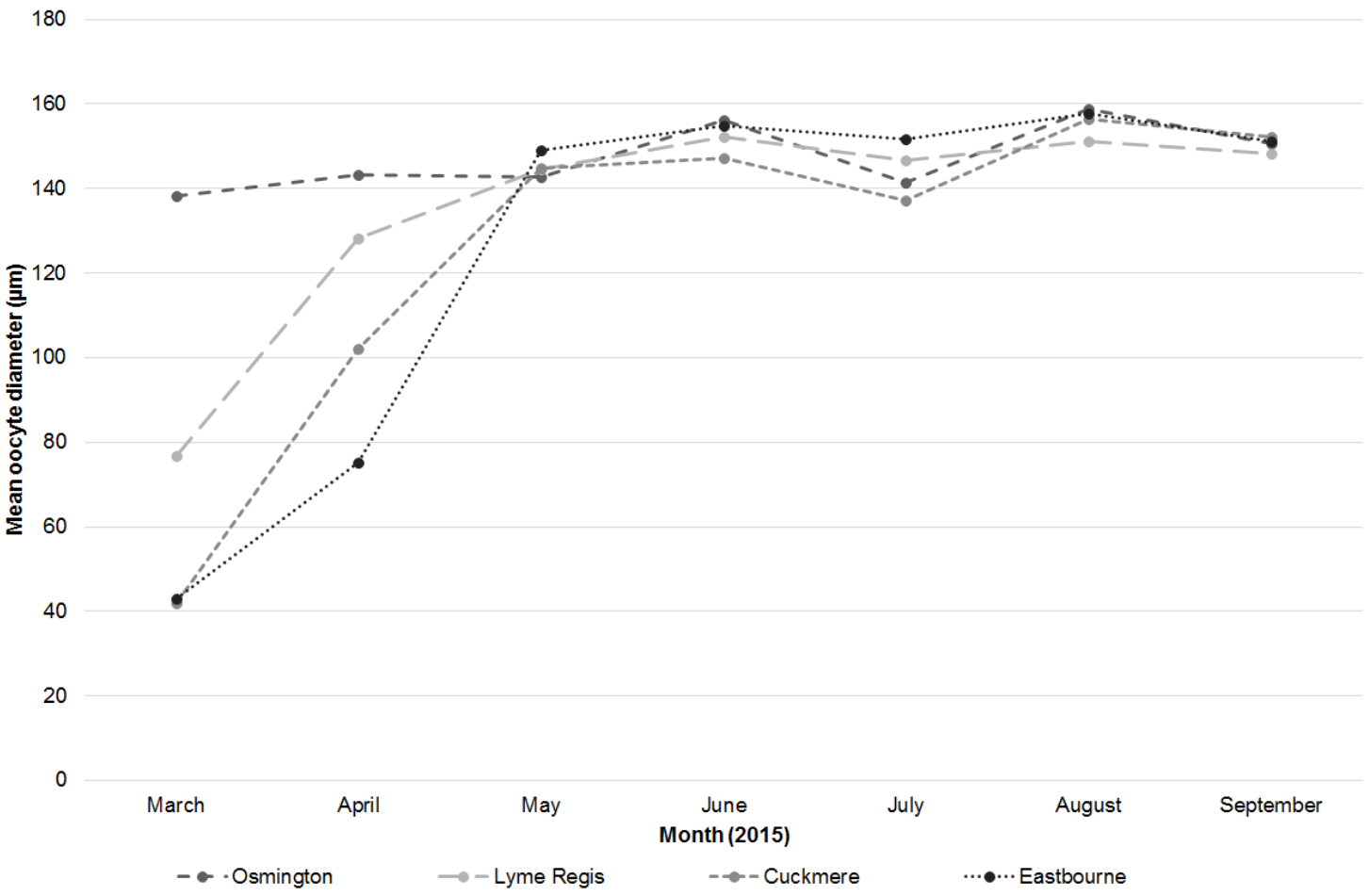


Figure 3.23: Mean oocyte diameters for each site over the seven months of the study. Error bars omitted for clarity.

From March the Osmington population already had large oocytes (Figure 3.24) and showed little growth over the spring and summer (138µm March, 158µm August). Lyme Regis oocytes had a mean of 77µm in March, Cuckmere and Eastbourne had the smallest oocytes at 42µm and 43µm. By April there were noticeable increases in oocyte size at all sites except Osmington which remained large. Cuckmere showed an almost 150% increase in size between March and April.

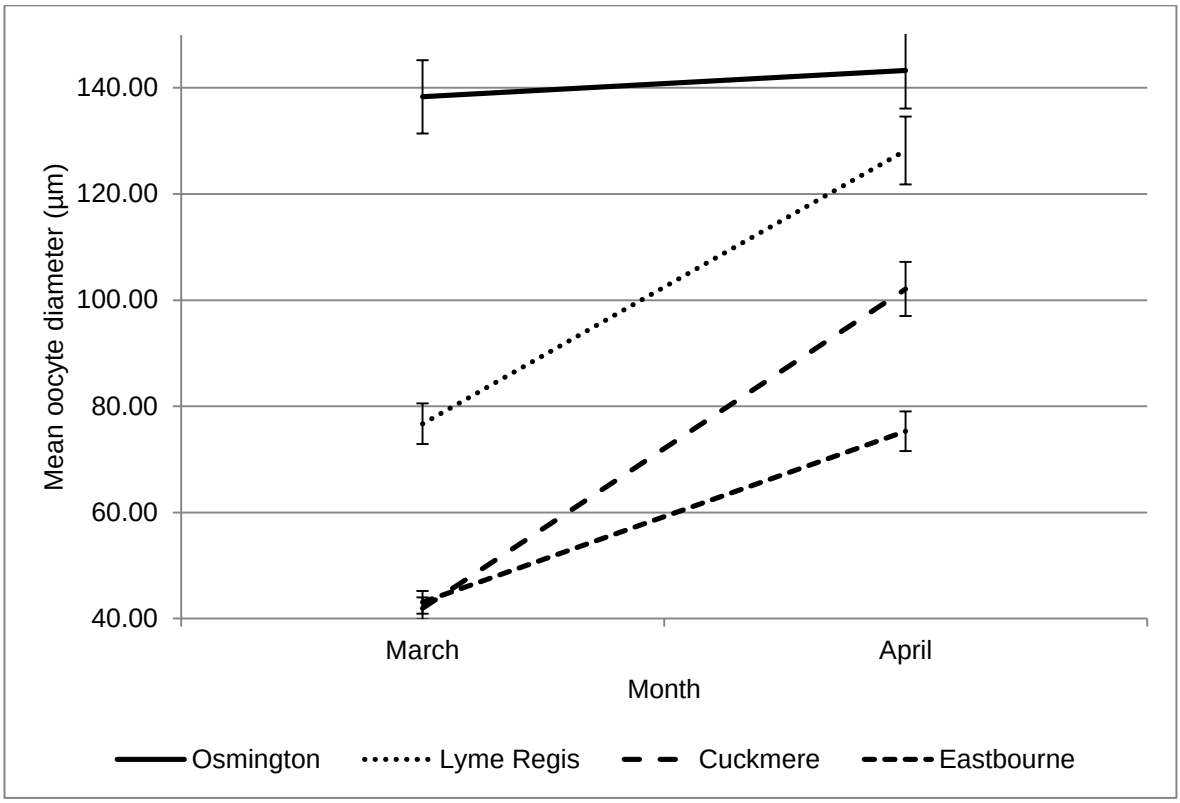


Figure 3.24: Mean oocyte diameters for March and April to show how growth rates differed between sites. Error bars at 95% confidence intervals.

From May onwards the mean oocyte diameters at all sites were similar, but a noticeable increase had occurred at Eastbourne of almost 100% (75µm to 149µm).

At all sites there was a slight decrease (between 3µm and 15µm) in mean oocyte diameter in July from the observations in June, however during August all sites showed an increase again. During August oocytes at three of the four sites were larger than they had been in June, Lyme Regis was marginally (<1µm) smaller.

During September all sites exhibited a reduction in mean oocyte size from the previous month. The means were similar across all sites (148.3µm to 152.1µm), with the smallest variance of mean (3.8µm) of the entire study.

Oocyte size-frequencies histograms were plotted for each month at each site and provide a visual overview of development (Figure 3.25).

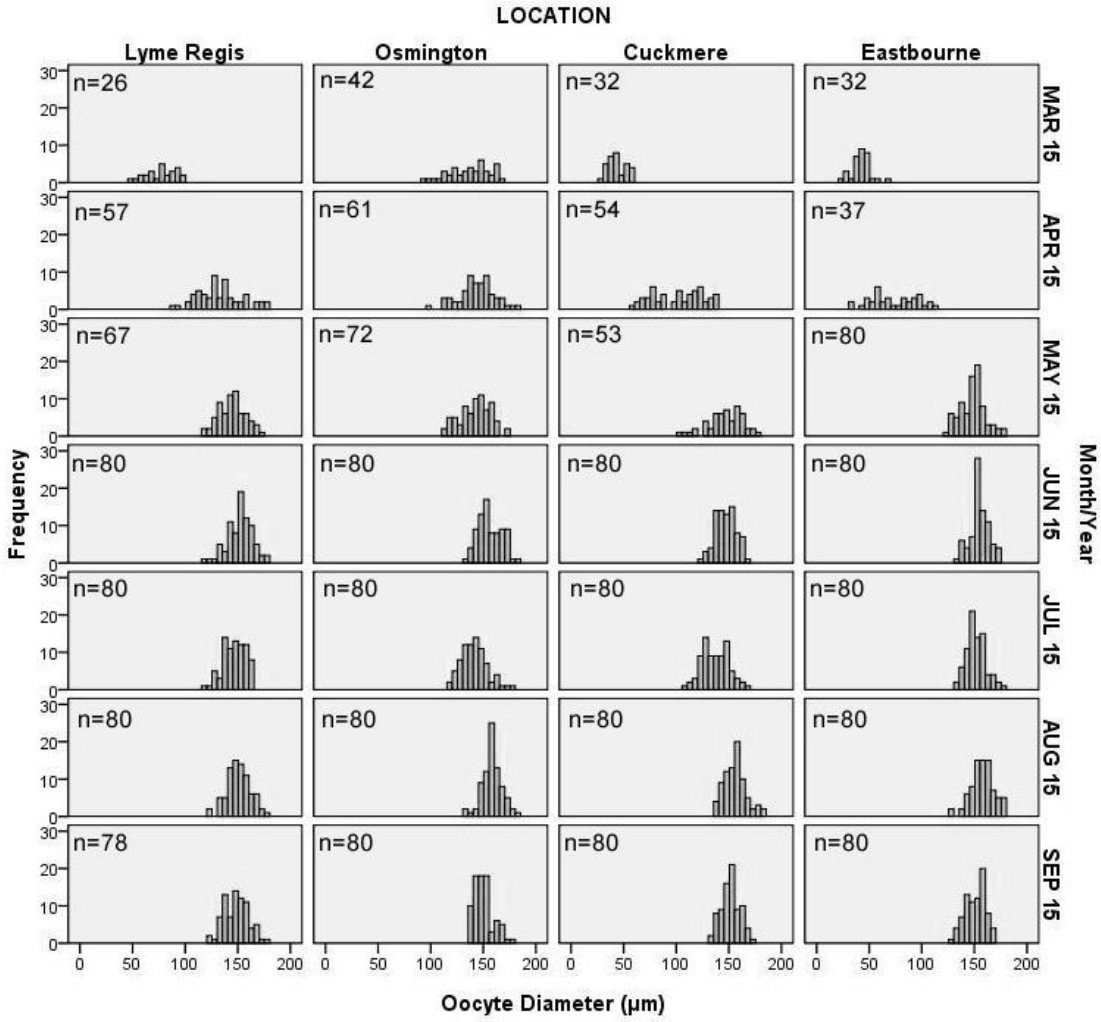


Figure 3.25: Oocyte diameter size/frequency histograms for each site/month.

A one-way ANOVA was used to test for statistically significant differences (Table 3.5) in mean oocyte size between sites. There were significant differences, however, there was no overall trend or consistency as the study progressed. September was the only month where no statistical differences were found between any site combinations. The only month where statistically significant differences occurred between all site pairings was

April, yet in May only one pair (Osmington and Eastbourne) showed a significant difference (p=0.05). The full output is presented in Appendix B.

	1-2	1-3	1-4	2-3	2-4	3-4
March	***	***	***	***	***	
April	*	***	***	***	***	***
May					*	
June		*		***		***
July	*	***	*		***	***
August	***	**	***			
September						

Table 3.5: Statistically significant differences of mean oocyte size identified using one-way ANOVA. 1 = Lyme Regis, 2 = Osmington, 3 = Cuckmere, 4 = Eastbourne. * denotes significance at p=0.05, ** denotes significance at p=0.01, *** denotes significance at p<0.001. Blank indicates no significant difference.

Mean oocyte diameters were plotted (Figure 3.26) for each development stage observed to determine whether oocyte size changed between stages. Only progression from Stage 2 (59µm) to Stage 3 (151µm) was accompanied with a noticeable increase in mean oocyte diameter (92µm), however the range of means within this stage was 35µm. Standard deviation reduced with each stage progression (Appendix C).

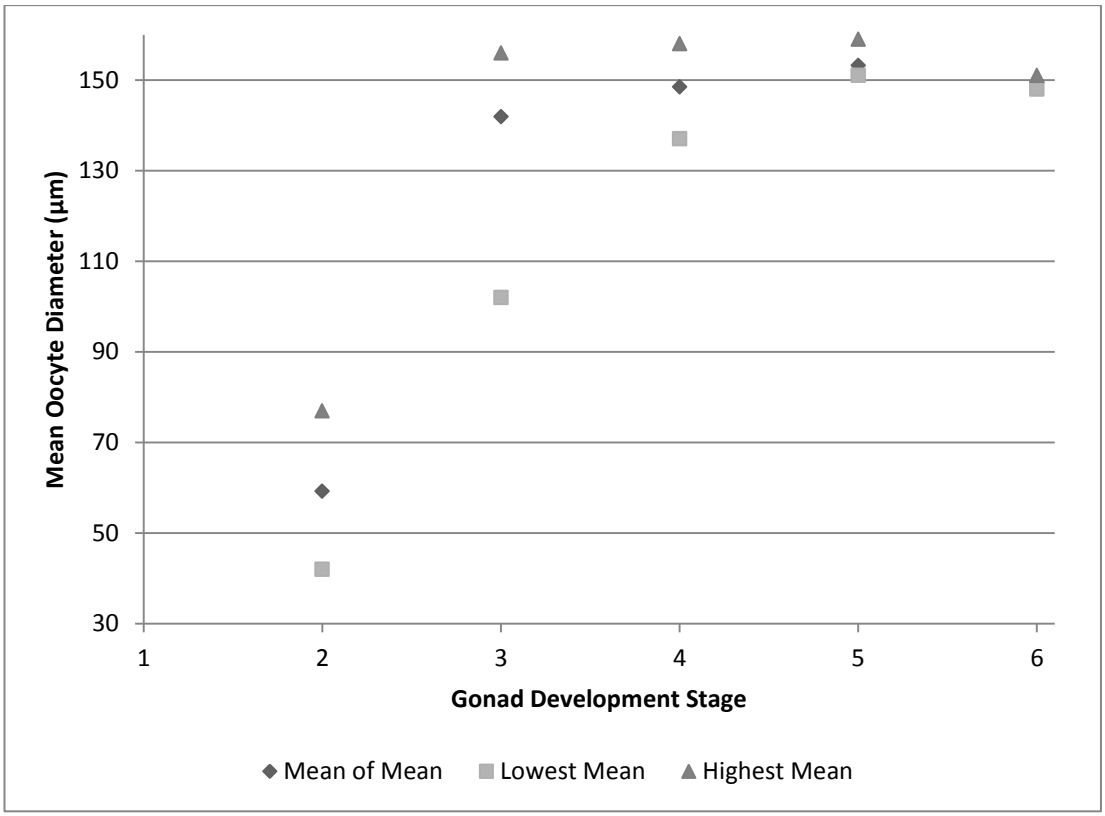


Figure 3.26: Mean oocyte diameters recorded for observed development stages (II to VI). Mean oocyte diameters for all sites and months was combined and the mean of means calculated. Lowest and highest means are plotted to show the range within each stage.

3.3.3 Relationship between sea temperature and oocyte size

Using a Pearson bivariate 2-tailed test there was a positive correlation between monthly sea temperature and mean oocyte diameter (r=*0.574, n=1891 p=<0.001*) when comparing the monthly sea temperatures with oocyte diameters (Figure 3.27).

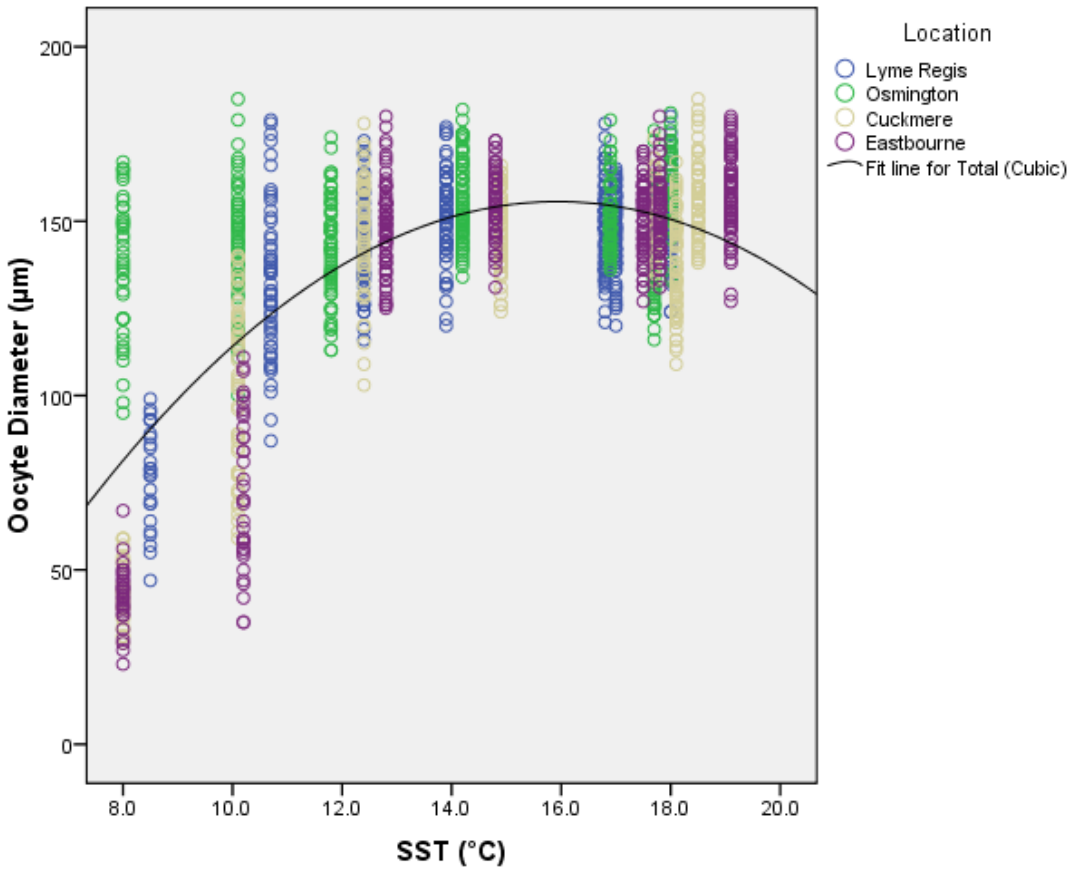


Figure 3.27: Relationship between sea temperature and oocyte diameter.

3.4 Discussion

The gonad staging process revealed reproductive development at different sites was not synchronised, and that there was a difference in rate of the progression between stages. However, development within each population was synchronised.

Statistical analysis (one-way ANOVA) of all oocyte diameters showed that there were differences in mean oocyte size between some sites during particular months, however, these differences were not consistent and changed from month to month. There were differences in the rate of oocyte growth as well as a difference in the timing when the oocytes in each population reached different sizes and maturity. An example of this is the growth of oocytes between March and May at Cuckmere and Eastbourne,

where both populations were at approximately 40µm during March, yet during April, Cuckmere had increased in size to over 100µm but Eastbourne were still only at 75µm. By May, Eastbourne oocytes (149µm) were larger than those from Cuckmere (145µm) and all other sites (Lyme Regis 145µm, Osmington 143µm). The analysis of oocyte diameters alone (ANOVA) is not satisfactory for detecting differences in oocyte development as some changes (e.g. colour of ovary and oocytes, formation of oocytes into a honeycomb fashion) are more difficult to quantify and are not accompanied by a change in oocyte size.

The oocyte measurements were similar to those of Garwood and Kendall (1985) who found that oocytes reached a size of 140µm to 180µm, but concluded that oocytes over 120µm can be considered mature. Despite extensive searching, there was no other literature found which contained information on the size of fully mature oocytes in *Gibbula umbilicalis*. Underwood (1972) looked extensively at gonad development and the only oocyte sizes mentioned relate to immature/developing cells. Underwood suggests the presence of a jelly coat around the oocyte signifies maturity. However, as pointed out by Garwood and Kendall (1985), this forms from between 70µm and 80µm, and its presence is irrelevant when attempting to determine whether oocytes have reached maturity. The related trochid *Tegula euryomphala* has a maximum oocyte diameter of approximately 156µm (Bastías 2014). Bastías suggests that this size is in the middle of a range (50µm to 300µm) described by Hickman (1992) for all trochid species. This may be an erroneous observation as when reviewing Hickman's work, it states that "*the typical mature trochean oocyte is a yolk-rich structure, of 150-300 µm diameter*" (Hickman 1992, p.249). Desai (1966) studied a similar species, *Phorcus lineatus (as Monodonta lineata)* and reported that oocytes reach a maximum size of between 165µm and 195µm. It should be noted that *Phorcus lineatus* is a larger species than *Gibbula umbilicalis* and can grow to over 30mm shell width (Williamson and Kendall 1981). Desai (1966) also states that *Gibbula* eggs reach a size of 120-150µm, however a specific species (if any) of *Gibbula* that this statement relates to is not given, nor is a source.

Methods used by Underwood (1971, 1972) were not repeated in this study as the technology now available makes the lengthy staining and sectioning processes unnecessary, and the task of measuring oocyte diameters can be completed in a matter of minutes using a digital microscope. Further, the use of a microtome to take a 2µm thick slice through tissue containing spherical oocytes between 40-180µm creates opportunity for erroneous measurements by taking slices of the oocyte at places anywhere other than at its widest. The likelihood of taking the central/widest portion of each oocyte would be low given that the oocytes are packed together in a honeycomb-like way. Mieszkowska (2005) used methods other than those involving histological techniques to determine reproductive cycles of *Phorcus lineatus (as Osilinus lineatus)* because of the time consuming nature of the work. Using a digital microscope allowed measurements to be taken with the oocytes intact and therefore ensured that each measurement recorded the maximum width of the entire oocyte rather than the width of a smaller portion of it.

Previous studies (Underwood 1971; Garwood and Kendall 1985) suggested that mean oocyte diameter is not appropriate for use to monitor reproductive development as their work found that individuals contained a range of different sized oocytes. Underwood (1971) measured oocytes and observed that females contained oocytes of a range of sizes simultaneously, both mature and immature. Garwood and Kendall (1985) did not observe this polymodal distribution, but rather bimodal, however they point out that during early stages of development the larger oocytes were unspawned from the previous cycle. One to four months after spawning had taken place, they noticed that the majority of oocytes present were small and it is quite possible that these were new oocytes forming for the next cycle. The consistent occurrence of different sized oocytes within an individual was not observed in this study; less than 5% contained oocytes noticeably larger or smaller than the majority. The presence of a small number of large oocytes in the earlier months was attributed to unspent oocytes from the previous cycle and these larger oocytes were excluded from the study. Of the few individuals with noticeably smaller oocytes present among the larger majority, the smaller oocytes were not measured on the basis that these were either new oocytes

developing for the following cycle, or possibly failed oocytes from the present cycle owing to the rarity of this occurrence. External fertilisation of an earlier release of previously unspent oocytes would of course require simultaneous release of male sperm, which is unlikely.

Growth of oocytes was well synchronised between individuals in each population and this is in line with observations made by Garwood and Kendall (1985). During July, some individuals were not dissected until they had been in the formalin for five days. In these individuals the female gonads had a purple colouration externally. This was further confirmed by checking some remaining tissue samples from June surveys which were not purple when viewed soon after immersion in formalin, but were when looked at again in September (Figure 3.28). However, some remaining samples collected in March and April were also looked at during September, yet these did not show the same change in colour. Some, but not all, of the oocytes also presented with a purple hue (Figure 3.29). The same method and equipment (including the same batch of formalin) was used for all samples. This staging process is to some extent subjective and dependent on experience, and may be influenced by the length of time of preservation.

The addition of expected oocyte sizes for each of the development stages would be useful by making the process more objective, however not only was growth between stages mostly low (stage II to III being the exception), the standard deviation in mean oocyte size was too high to reliably associate any one stage with an expected oocyte size when means of each stage were similar.

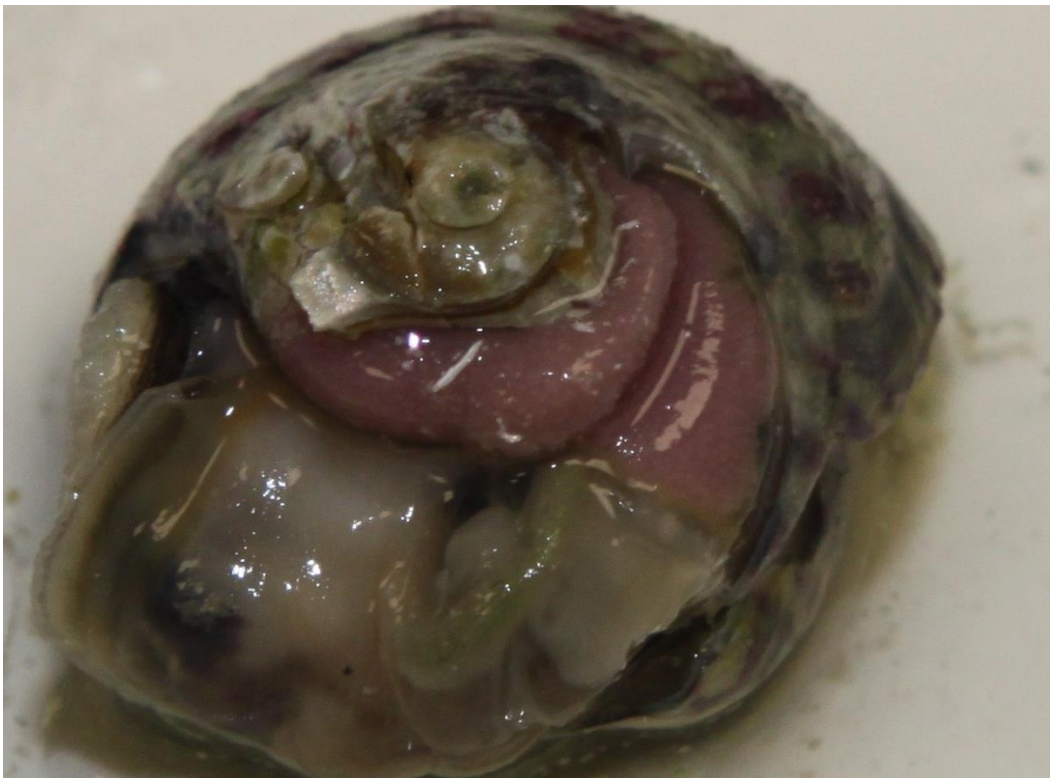


Figure 3.28: Purple appearance of ovary. This sample was collected during June from Cuckmere but was not used in the oocyte analysis. Photograph taken in September.

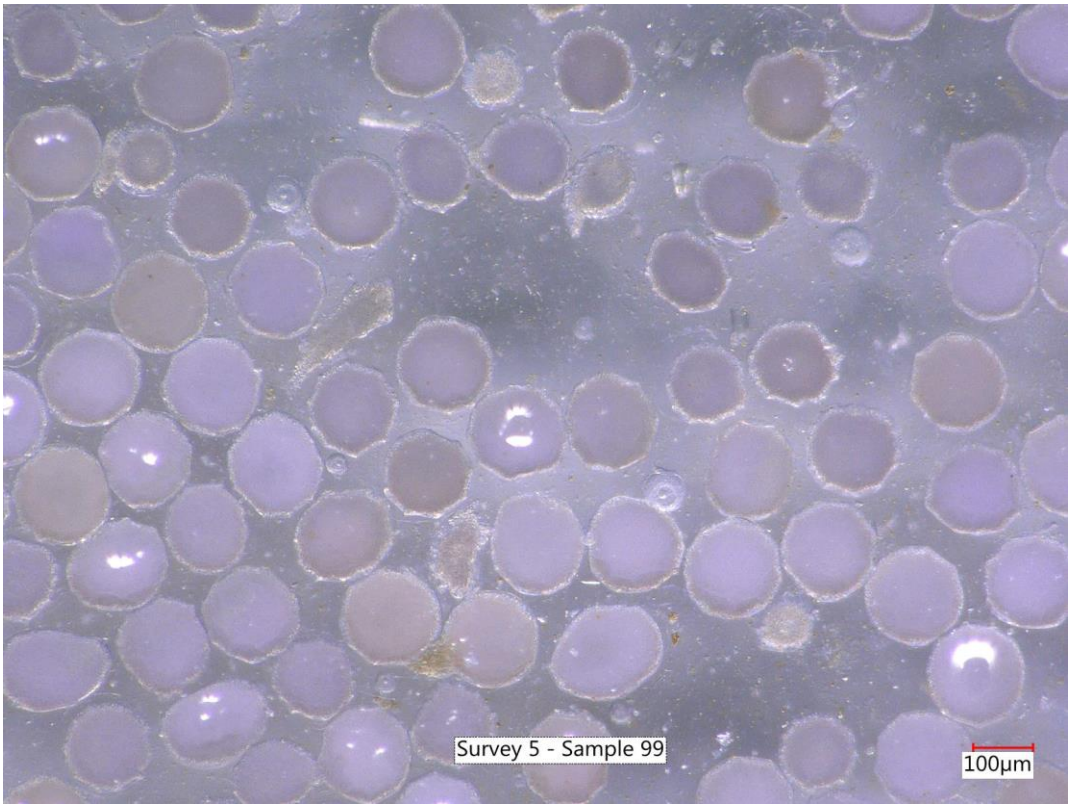


Figure 3.29: Oocytes with purple appearance (sample collected in July from Eastbourne).

The positive correlation between sea temperature and oocyte size was expected as it was already known that gonad development and oocyte growth occurs during spring when sea temperature begins to increase (Garwood and Kendall 1985) and these result support previous findings. The eastern basin of the Channel has a wider temperature range than the west; winter minimums are lower and summer maximums higher (Rayner et al. 2003). It has been hypothesised (Hawkins et al. 2008; Herbert et al. unpublished) that the recent range extension of *Gibbula umbilicalis* along the south coast of England is due to the rise in mean sea temperature and milder winter temperatures.

Possible mechanisms for this are:

(i) Longer reproductive period and the possibility of multiple spawnings, increasing the probability of successful fertilisation;
(ii) Increased larval output and higher settlement;
(iii) Milder winters will enable greater spat survival and greater recruitment, leader to persistent populations.

The annual heating and cooling cycle of the sea in the English Channel means that for several months of the year the sea is too cool and reproductive development is limited to one cycle each year, with spawning occurring at the end of summer. In areas where the seas are warmer (off the coasts of Portugal and Spain), brooding occurs more than once a year and there are multiple spawnings (Bode et al. 1986). The higher temperatures also reduce the risk of juvenile mortality (from a thermal perspective) negating the need for breeding to occur at a specific time to coincide with adequate temperatures for juvenile survival.

Sea temperatures fell between August and September at all sites, (decreases of 1.2°C at Lyme Regis, 1.1°C at Osmington, 0.8°C at Cuckmere and 1.6°C at Eastbourne) however, spawning was only observed to be in progress in the western basin at Lyme Regis and Osmington. In some species (Crothers 2001) the attainment of maximum temperature can trigger

spawning. However temperature data obtained in this study is not of sufficient temporal resolution from which to draw conclusions on what the trigger may be; spawning may have begun up to 27 days before the September survey.

Given that low winter temperatures are a risk for juveniles (Kendall and Lewis 1986), and that the eastern basin of the Channel experiences colder winter sea temperatures than the west, it might be expected that those populations in the east would spawn earlier, hereby giving the settling juveniles as much time as possible to grow and increase the likelihood they will survive the first winter. That is on the assumption that smaller and younger juveniles are at more risk than larger, older individuals. However, it was western sites that were the first to spawn, and this suggests that the delayed spawning in the east leaves those populations vulnerable to recruitment failure, as delayed settlement may increase post-settlement mortality. At the end of summer the sea temperature begins to fall sooner in the west than the east, and it is possible that this delay, which occurs in the same region as delayed spawning, may promote recruitment by reducing post-settlement mortality.

3.5 Conclusion

This aim of this Chapter was to understand when different reproductive stages of *Gibbula umbilicalis* occur at four different sites on the south coast of the UK, and whether there were differences (rate of development and timing) between those sites. The effect of temperature on reproduction was also considered. Reproductive development of females was not fully synchronised between populations; not only did different populations reach different stages at different times but the duration spent at each stage differed between sites. Individuals at Osmington contained large oocytes from the first survey in March, while those at the other sites which contained smaller oocytes in March were observed to show rapid oocyte growth (though not at the same rate as each other) and by May their oocytes were larger than Osmington. The early development observed at Osmington, which saw oocyte size remain stable for the duration of the study, did not result in the site being the first to spawn. There was a positive correlation

between sea temperature and gonad development. The results of this study show that reproductive development and spawning timings are localised, and although populations in the eastern basin spawn later than those in the west, a delayed drop in sea temperature in the eastern basin at the end of summer may provide protection against post-settlement mortality.

Until now, reproductive development and spawning in the eastern English Channel has not been investigated to understand when it occurs or to compare it with populations in the west that have been established longer. The results of this study show that reproduction is not simultaneous along the English Channel and that there is a link between sea temperature and oocyte development and spawning.

4. Population Recruitment and Growth

4.1 Introduction

Following the pelagic larval stage, veligers settle if suitable substrate is available, but not all individuals that settle will survive. Post-settlement mortality can, among other factors, be the result of predation, lack of food, or inadequate environmental conditions (temperature, salinity) (Hunt and Scheibling 1997). Recruitment definitions vary between species and from study to study, including the point in time which an individual is first detected/observed (Caselle and Warner 1996), has survived an initial period of high post-settlement mortality (Booth and Brosnan 1995), has reached (Walters and Juanes 1993) or is likely to reach adulthood or sexual maturity (Menge and Sutherland 1987) or has reached a specific size (Rodríguez et al. 1993) or age (Myers et al. 1997). Wave exposure has an influence on the morphology and distribution of many rocky shore species, including gastropods (Ballantine 1961; Vermeij 1973). Gastropods on shores exposed to higher levels of wave action are likely to have shorter, wider shells than individuals of the same species on sheltered shores (Frid and Fordham 1994). *Gibbula umbilicalis* has a flat shell in comparison to similar species, and, although this is a trait for survival on an exposed shore, it is also a predator defence (Cotton et al. 2004). When temperatures are low *Gibbula umbilicalis* is confined to rock pools which reduces feeding activity, and as a consequence growth is restricted (Williams 1964).

From around the year 2000 the range of *Gibbula umbilicalis* has extended eastwards on the English side of the Channel (Hawkins et al. 2009; National Biodiversity Network 2015; Herbert et al. unpublished). Previously only found as far east as the Isle of Wight, for the past 15 years the species has now been observed at Littlehampton, Seaford, Eastbourne and as far as Kent (Herbert personal com.). This range extension has coincided with an increase in mean sea surface temperature (SST) and, importantly, winter minimum temperatures (Mieszkowska et al. 2006, Hawkins et al. 2008, Herbert et al. 2009, Keith et al. 2011) (see also Chapter 2). It has been

suggested that temperature was the most likely cause for the previous absence of the species in the eastern basin of the Channel (Mieszkowska et al. 2006). Lack of suitable habitat (Crisp and Southward 1958; Herbert and Hawkins 2006), hydrographic barriers restricting larval supply to the shore (Crisp and Southward 1958; Herbert et al. 2009; Keith et al. 2011) or intense pressure predation on newly settled juveniles may have also played a role. It is considered that temperature, specifically the winter minimum sea temperature, is most critical because of the risk it poses to the survival of juveniles (Kendall 1987). Keith et al. (2011) estimated that a minimum temperature of 7.98°C is required for almost all individuals to survive the winter; yet a temperature of 7.4°C could cause almost complete mortality. However, the duration that this temperature would need to persist to have this effect is not given. The results of a laboratory experiment suggested that exposure to temperatures of -5°C for 6-24 hours will lead to over 50% mortality (Southward 1958). The only opportunity for the species to be subjected to such extreme low temperatures along the south coast of the UK is during low tide when exposed to cold air. Along the open coast, the sea in this region does not freeze although ice has been observed to form in the upper reaches of estuaries and harbours. Further, the duration of exposure varies depending on tidal activity and their position on the shore. Following the exceptionally cold winter of 1962-1963, Crisp (1964) failed to locate any living *Gibbula umbilicalis* on the Isle of Wight, and only one individual at Osmington Mills, where previous searches had recorded over 100 individuals per m^2. At Lyme Regis *"dead shells of the species littered shallow pools in thousands"* (Crisp 1964 p182).

To understand whether new populations of *Gibbula umbilicalis* might now be considered established, the population structure was investigated at four sites on the English side of the Channel (see Chapter 2 for details). The presence of juveniles (maximum basal shell diameter (MBD) less than 10mm) is an indicator of recent (within the previous 12-18 months) successful recruitment (Williams 1964). By measuring the shell MBD it is possible to track the growth of juveniles (young of the year) over time to determine survival of the cohort and entry to the adult population. Evidence

of recent and frequent recruitment could show that the new populations are now ecologically established, and depending on density able to withstand pressures of occasional disturbances such as unusually cold winters which might otherwise cause the complete loss of populations, as observed by Williams (1964).

4.2 Methods

Following the MarClim protocol (Mieszkowska et al. 2006) which is comparable to the method of Kendall and Lewis (1986), five searches, each lasting three minutes, were carried out monthly at each site between March and September 2015. Any rocks that were moved during searches were returned and care taken not to crush any organisms. The Maximum Basal Diameter (MBD) of all individuals collected was measured on-site using digital callipers, after which the animals were returned to the shore, with the exception of those required for the reproduction study (Chapter 3).

4.3 Results

Limited data collected in late spring and early summer during 2010 (R Herbert unpublished data) and 2012 (R Noke unpublished data) for a single site in each basin provides a baseline to which populations can be compared (Table 4.6). These searches used the same method as the current study. There was a considerable increase in the number of snails found (64%) between 2010 and 2012 at Osmington, and a large (50%) decline at Cuckmere. From 2012 to 2015 there was a reverse in the trend, with Osmington decreasing by 53%, but Cuckmere increased 50%.

	May-2010	Apr-2012	May-2015
Osmington	14	23.4	10.4
Cuckmere	11.8	6.4	8.8

Table 4.6: Mean number of individuals found per minute of searching after five three-minute searches. Amounts are only representative of the months indicated.

Juveniles (MBD<10mm) were found at all sites in each month (Figure 4.30) with the exception of Eastbourne during April where the smallest individual found was 10.5mm. The number of juveniles recorded each month at each

site varied. During March only one juvenile was found in Eastbourne and three in Cuckmere, but they were more common in Lyme Regis (11) and Osmington (41). At Eastbourne and Cuckmere there was an increase in the presence of juveniles as the study progressed, but in Lyme Regis and Osmington juvenile numbers peaked during May.

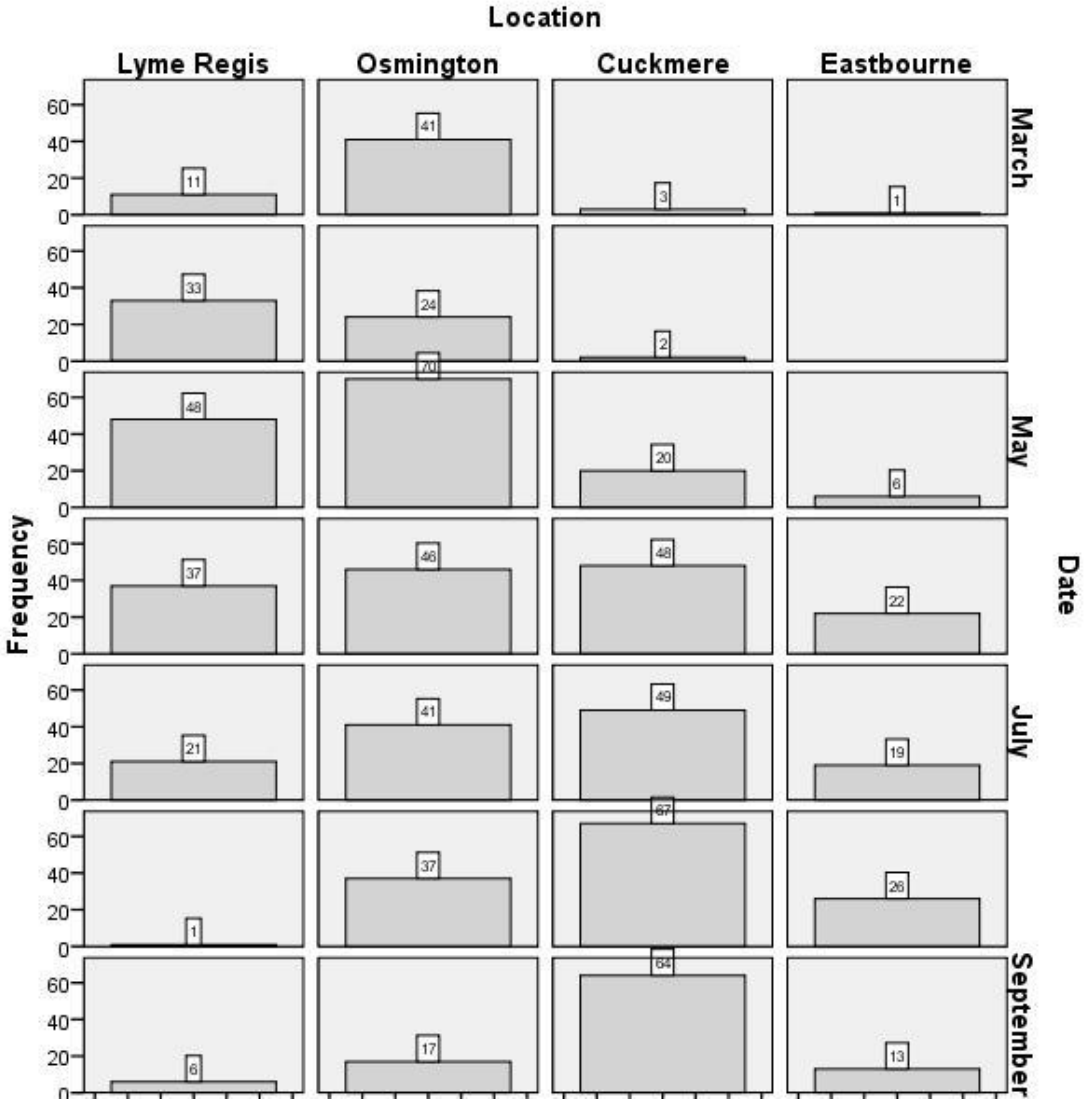


Figure 4.30: Number of juveniles found during each survey at each site.

The mean MBD of juveniles (Figure 4.31) at each site increased overall between March and September. Eastbourne showed the largest increase in juvenile mean MBD over the study at 3.4mm between March and September, and Cuckmere the smallest increase at 0.7mm. The largest mean MBDs for

juveniles were observed in August at all sites except Cuckmere, where the largest mean (8.7mm) was seen in September.

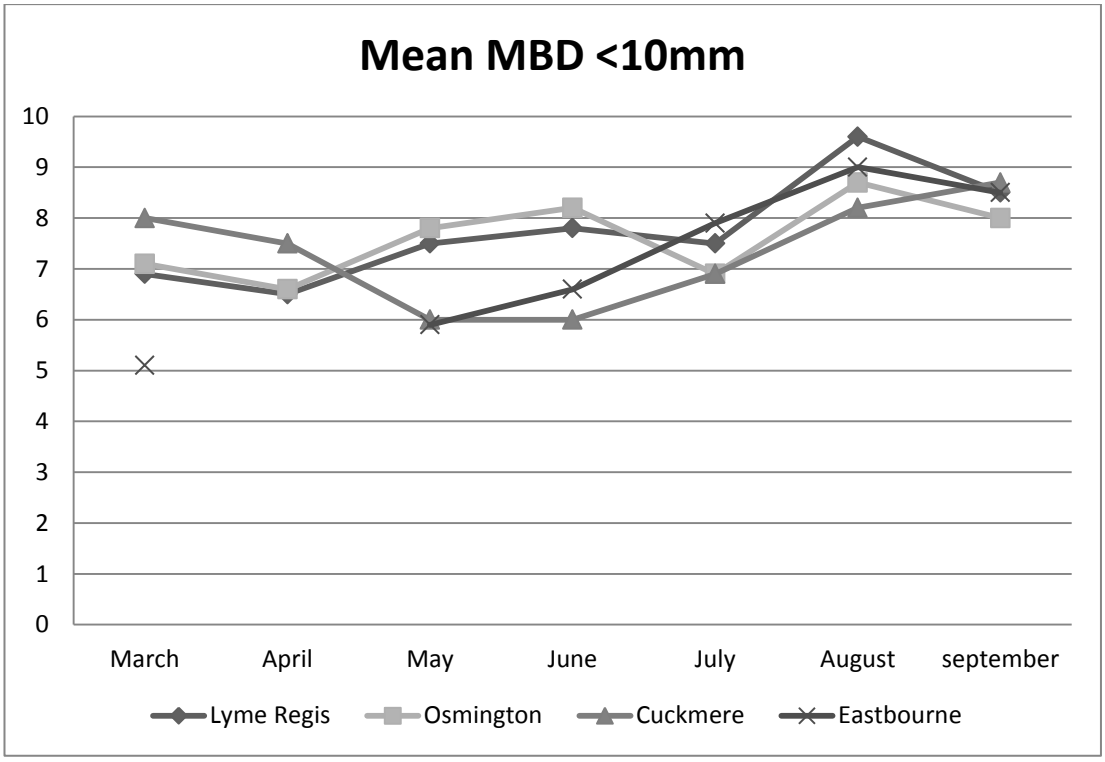


Figure 4.31: Mean MBD for juveniles (<10mm) at each site each month.

By plotting size-frequency histograms for each survey (Figure 4.32), multiple modes are visible during some months at some sites, and the mode of the younger cohorts can be seen to increase in size over time as the juveniles grow.

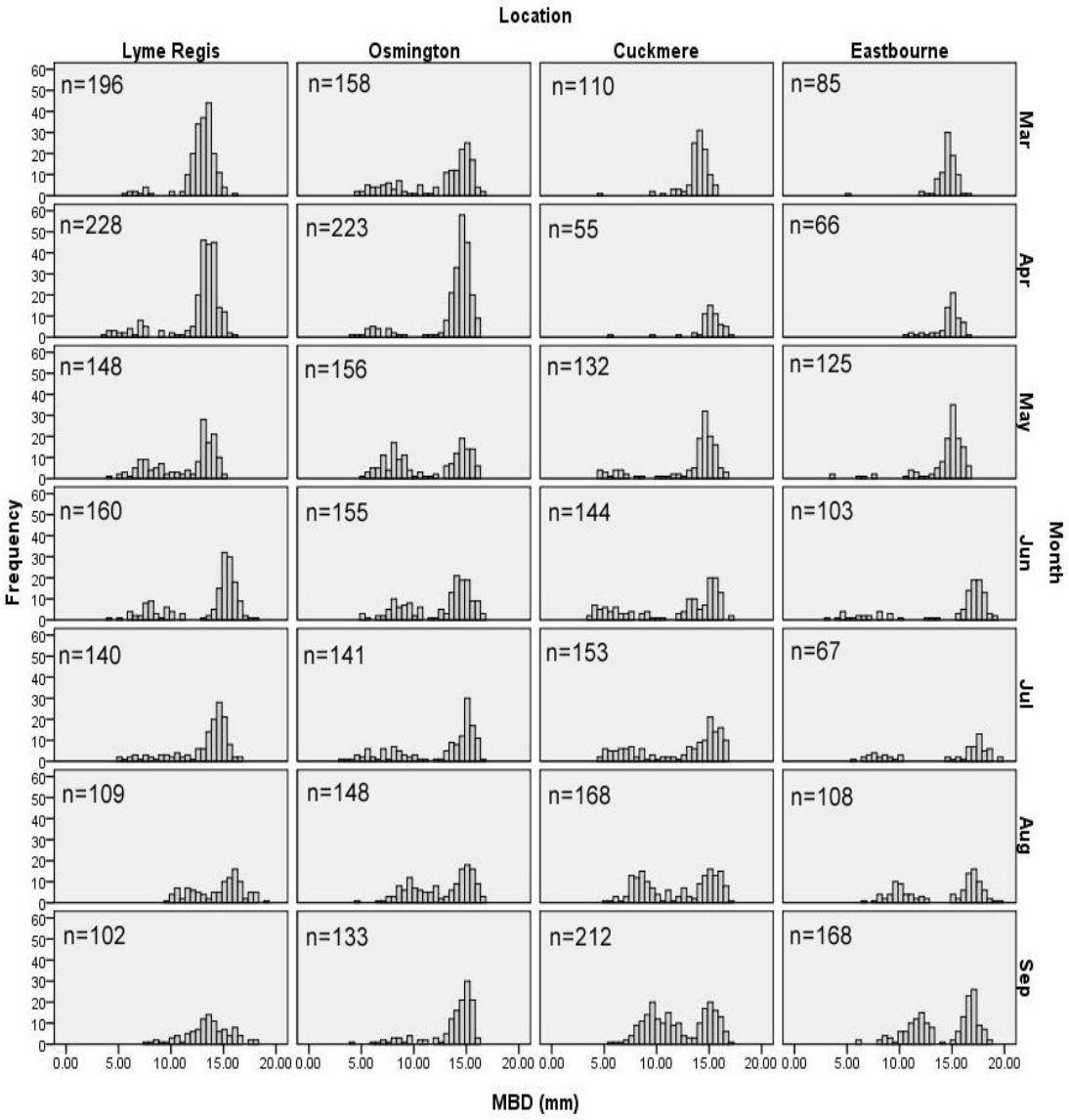


Figure 4.32: Monthly size-frequency histograms showing population structure and growth of 2014 cohort and older cohorts. MBD denotes shell Maximum Basal Diameter.

Over the duration of the study more individuals were found at Osmington (1114) than any of the other sites. Searches at Lyme Regis located 1083, Cuckmere 974 and Eastbourne 722 over the seven months. With the exception of September, searches at Eastbourne located the fewest individuals. At the start (March and April) Lyme Regis and Osmington had far greater numbers than Cuckmere and Eastbourne, but during May and June survey totals were more similar; numbers found at Lyme Regis and Osmington fell while those at Cuckmere and Eastbourne increased. July, August and September saw Cuckmere produce the greatest numbers and in September the number found at Eastbourne was the fourth largest out of all

28 searches. Osmington showed a small decrease between July and September while Lyme Regis fell by over a quarter. The number of individuals located during each survey is presented in Figure 4.32.

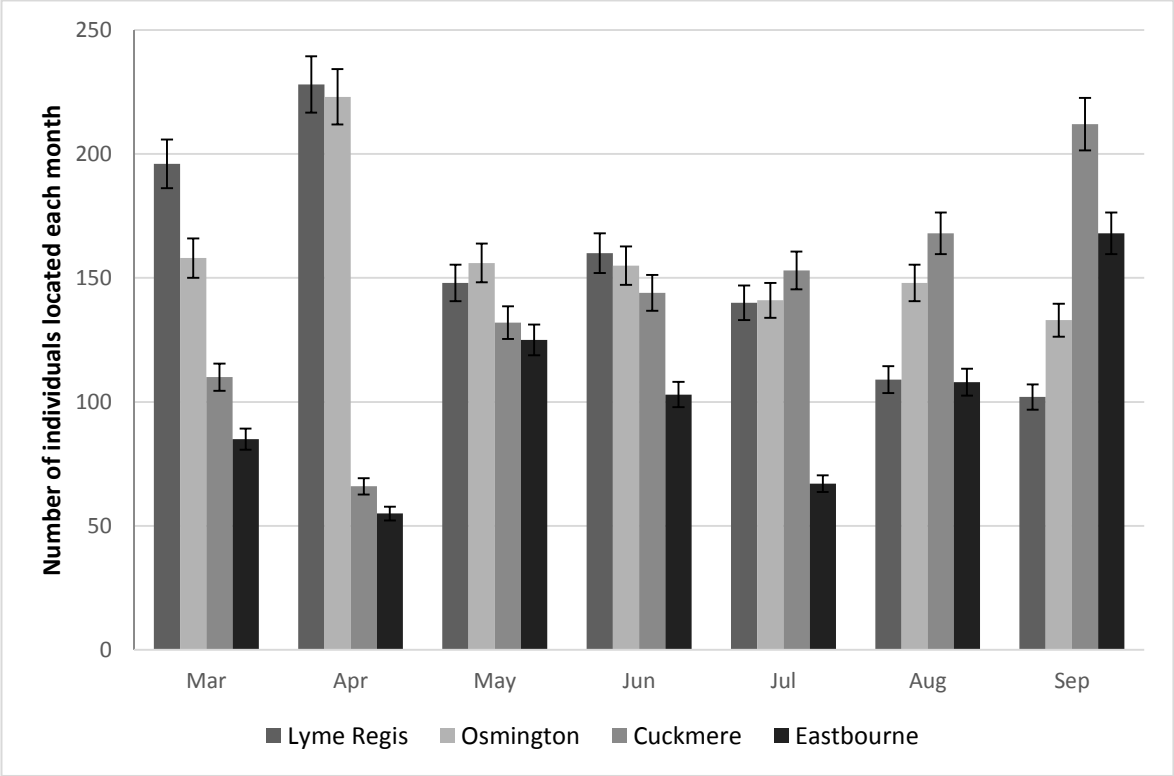


Figure 4.33: Number of individuals found at each site during each visit. Error bars at 95% confidence.

Eastbourne had the largest mean MBD (14.4mm) overall and also the fewest individuals (722 in total, 6.8 per minute of searching). Eastbourne also had the lowest number of juveniles both as a percentage of all individuals found there (12%) and the actual quantity of juveniles (87). Figure 4.34 shows the proportions of juveniles:adults for each site over the duration of the study. The largest individual found throughout the study (19.7mm) was at Eastbourne. The site with the lowest mean MBD was Cuckmere (12.6mm), although Osmington and Lyme Regis were only marginally larger at 12.7mm and 12.9mm respectively. With juveniles (MBD <10mm) removed Lyme Regis had the lowest mean MBD (13.9mm). Using MBD at the 90th percentile to reduce bias caused by the number of juveniles, and the number of individuals located each minute, the results (Figure 4.35) showed that the general trend was that smaller populations contained larger individuals.

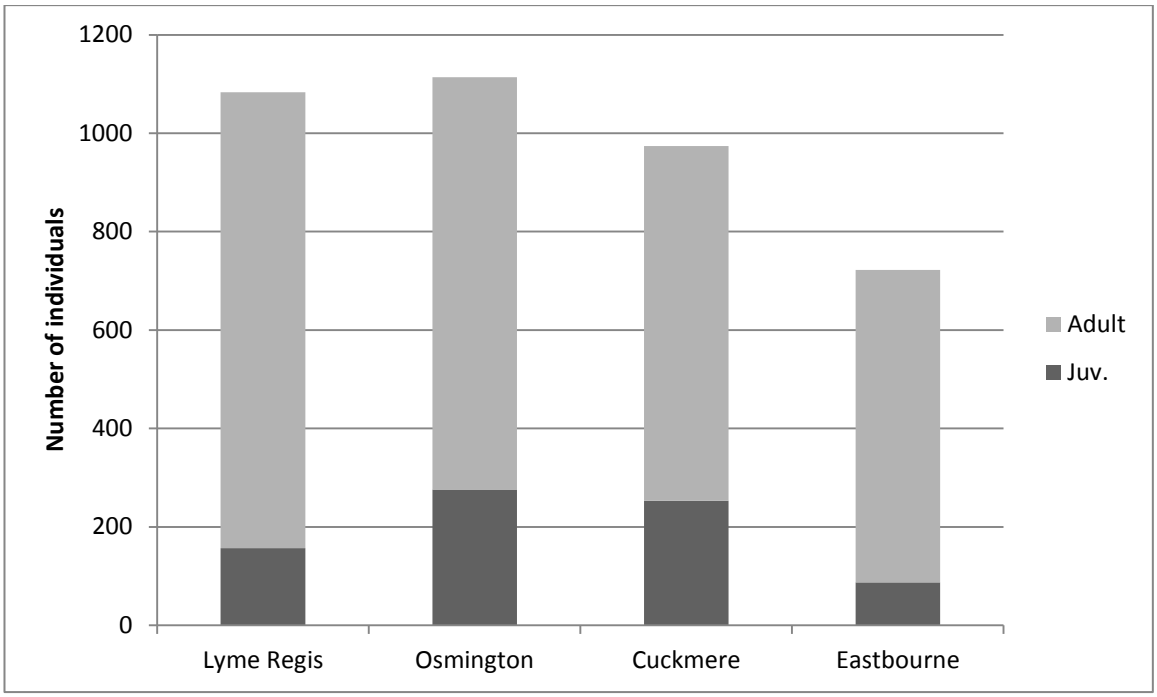


Figure 4.34: Total number of individuals found throughout the surveys (March-September) and proportion of juveniles.

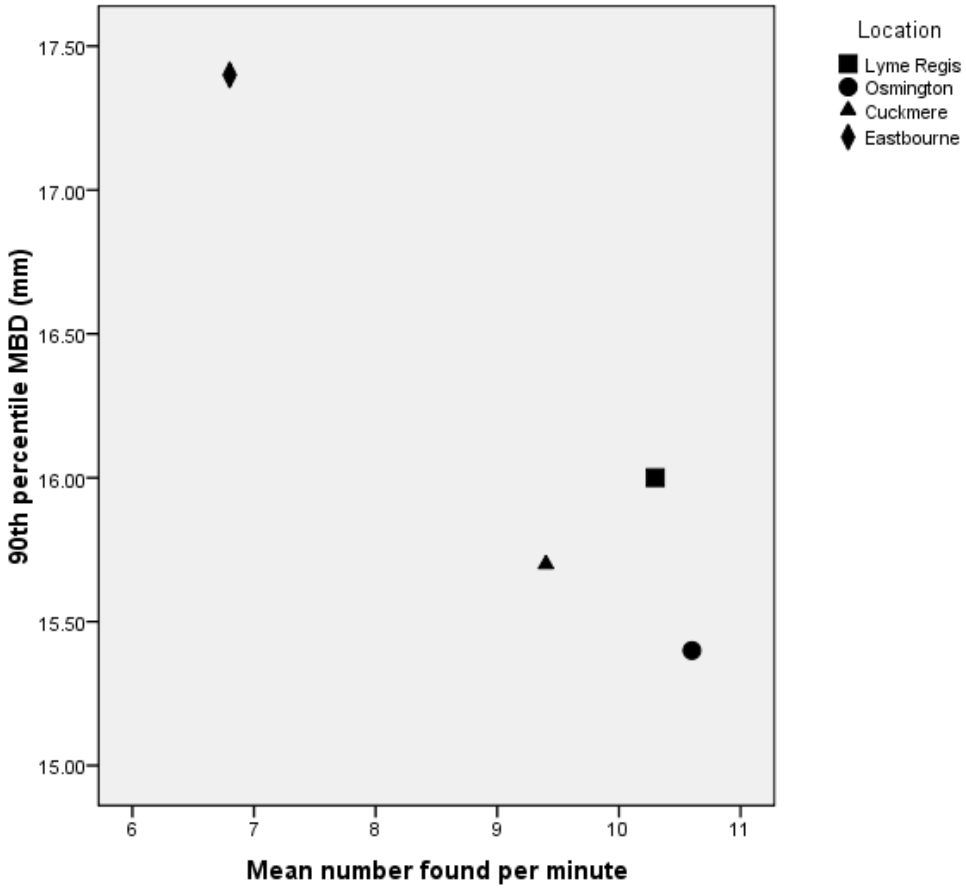


Figure 4.35: Comparison of mean MBD at the 90th percentile and abundance (based on number of individuals found per minute of searching).

4.4 Discussion

During the field surveys the weather was good, with each survey taking place in dry, calm conditions. Wet weather is understood to cause trochids to seek shelter under rocks (Crothers 2001) or stay submerged under water during low temperatures or in high winds (Little et al. 1986). Field surveys under different weather conditions would likely produce variable results and make it difficult to draw conclusions if trying to compare two areas. There is a relationship between age and size, however the results show that different populations display different growth/size characteristics. This is the result of differences in localised pressures such as the quality of habitat or intraspecific competition. Therefore, the size of an individual should only be used as a guide to determine age. Ideally, size-frequency distributions should be consulted to determine size of juveniles within any month, rather than the standard >10mm threshold MBD for when individuals can be considered mature.

From the evidence of juvenile recruitment, size-frequencies and large populations at the eastern sites of Cuckmere and Eastbourne, the species is now considered established at these eastern localities in the Channel. This has only occurred because sufficient numbers of juveniles have both recruited and survived here. New sites may still rely on the arrival of larvae from other areas to maintain or increase the populations as their own reproductive efforts may result in their larvae being transported away. If connectivity between an external larval source and its destination was interrupted, populations dependent on this source of larvae would eventually disappear. The degree to which these populations rely on external larval input is unknown. According to the National Biodiversity Network (2015) there are records of *Gibbula umbilicalis* present, intermittently, along the east coast of Britain from the south-east tip in Kent up to Scotland. However, records on the north-east coast are probably incorrect and require verification (Herbert pers. com.). Lack of confirmed sightings should never be given the same weight as an unsuccessful search for the species. Large gaps in their actual distribution will exist as a result of the presence of long stretches of sandy shores along parts of the North Sea coast. The creation of new habitats in

the form of artificial structures (sea walls, groynes) may act as stepping stones facilitating range extensions as observed in other species. However, until such a time that these populations can be confirmed, whether they originated from the north or south will be unclear.

The number found during the September search at Osmington (133), was not greatly different from the previous two searches (148 during August, 141 in July). If the number of juveniles found at each site is a true reflection of recruitment, the later detection and lower numbers of juveniles in the eastern cell would indicate that populations in the western cell reproduce earlier and achieve higher levels of recruitment.

Eastbourne had the largest mean MBD over the study and this can be attributed to two factors. Firstly, searches at Eastbourne located the fewest juveniles and this increased the mean MBD size as the data contained a greater proportion of adults than other sites. Secondly, decreased intraspecific competition (a result of the low population) can result in individuals reaching a larger size than in areas where populations are denser. After eliminating juveniles (<10mm) from the data (for all sites) the mean MBD (15.3mm) at Eastbourne was still the largest of all the sites. The observed low number of juveniles at Eastbourne could be the result of a restricted larval supply limiting the numbers of individuals with the opportunity to settle. The presence of Beachy Head, the major headland south-west of Eastbourne could be restricting larval supply to the shores as headlands appear to create barriers for other species (Crisp and Southward 1958; Herbert et al. 2009; Keith et al. 2011). The substrate at Eastbourne contained less loose material than other sites and subsequently fewer cobbles that the juveniles prefer. This limited availability of suitable habitat is likely to be a contributing factor affecting settlement and recruitment. Further, the texture of the rock surface at Eastbourne is visibly smoother than at the other sites, with many large areas of flat chalk ledges. There is evidence that the grazing rate of *Gibbula umbilicalis* on smooth rock is only half of that of a rough surface (Griffin et al. 2009), which may account for lower populations. Whilst the roughness of the rock at the different locations was not quantified in this study, the stark contrast between Eastbourne and the other sites is such that

it was noticed upon arrival at the shore, so much so that there were initially some doubts as to whether the species would be present. Rock type and roughness can influence the settlement and mortality of the Lusitanian barnacle *Chthamalus montagui* (Herbert and Hawkins 2006) and this may contribute to the species distribution being mainly limited to sites west of the Isle of Wight where more suitable rock occurs.

Although Lyme Regis had a low proportion of juveniles similar to Eastbourne, the overall number of individuals was greater at Lyme Regis than Eastbourne. The greater abundance at Lyme Regis can explain why the mean MBD was lower than Eastbourne despite juveniles at both sites accounting for similar proportions of the population.

Population size-frequency distributions with missing cohorts could be the result of infrequent recruitment or post-recruitment mortality including predation. This might occur between the early juvenile stage, when they reside under rocks out of reach of larger predators and the larger adult stage where they might be less desirable by predators because of their size (Underwood and Fairweather 1989). Although juveniles are more abundant in some areas than others, they were present at all sites and are evidence that recruitment has been successful in the last 12-18 months. The growth of the young cohorts over the course of the study is shown in the size-frequency histogram which indicates the smaller cohorts increasing in size between surveys at each site (Figure 4.32). The low number of juvenile individuals, however, does not allow the modes or different cohorts to be statistically analysed reliably (Kendall and Lewis 1986).

Temperature increases during the late 1990s are considered a driver of the eastward range extension. Summer temperatures were in the tolerable range in the eastern basin of the Channel before this period. Winter temperatures, considered the most important for survival of juveniles, have increased winter mortality is currently not as limiting to population growth. However, the proximity of the eastern basin to the cooler North Sea exposes populations to the effects of occasional cold winters and high mortality of juveniles may still occur. It is possible that the increased temperatures during the 1990s

allowed the eastern range-edge populations on the Isle of Wight to increase to greater levels than before, and therefore increase the likelihood of these populations seeding new sites with an increased volume of larvae. Reproductive development in eastern populations is delayed compared to that of populations in the western basin (Chapter 3.3.1). However, the differences are only marginal. Sea temperatures along the coast are also not synchronised (Chapter 2.2, Figure 2.9) and the fall in temperature during autumn occurs later in the east than in the west. The delayed fall in sea temperature coinciding with later juvenile settlement will offer some protection against winter mortality.

Competition for food can come not only from other individuals of the same species, but also from other similar species; *Phorcus lineatus, Littorina littorea* and *Gibbula cineraria* are known to co-exist with *Gibbula umbilicalis* in the western Channel yet no similarities in food preference have been identified (Hawkins et al. 1989; Crothers 2003). *Gibbula cineraria* are usually found lower down the shore therefore significant interspecific competition is unlikely. If other grazing species with a food preference similar to that of *Gibbula umbilicalis* already dominates an area, it could be that inter-specific competition is preventing *Gibbula umbilicalis* from becoming established. The seagrass *Zostera marina* is a known food source for *Gibbula umbilicalis* and this is more common to the west of the IoW than the east (Tyler-Walters 2008).

The timed searches used in this study replicated previous unpublished work allowing the results from May to be compared to data collected in May 2010 and April 2012. There were alternating increases and decreases of at least 50% in the number of individuals found from one year to the next at both Osmington and Cuckmere, however the direction of swing was never the same at both sites; as Osmington increased, Cuckmere decreased and vice versa. The gap in time between data points in this comparison is two and three years, meaning the large variations are not simply a biannual cycle. The scale of variability is similar in both locations, indicating that the "new" population in Cuckmere is no more or less dynamic than Osmington which has been established for longer.

In geological terms the English Channel is still a young feature, and it could be that establishing an ecological balance is something which remains in progress (Southward et al. 1995). It is possible that the penetration of hydrodynamic dispersal barriers around the Isle of Wight and subsequent settlement and recruitment on shores on the south east coast of England has been supplemented by settlement as a result of spawning of populations on the French coast, which have been known to occur further east (Crisp and Southward 1958). The water in the Channel moves westwards with a falling tide draining into the North Atlantic, and eastwards as the tide rises again. The east-west movements are not equal and overall there is an eastward flow of water (Ayata et al. 2010). There is no north-south tidal movement of water between France and the UK. Wind direction, which although predominantly is from the south-west, can come from any direction and alter the flow of water in the Channel (Salomon and Breton 1993). With distances between French and UK shores as low as 30km, larvae could travel that distance in under 18 hours at a rate of only 1 knot. No literature has been found which has considered this scenario in the context of *Gibbula umbilicalis*. Through the use of DNA analysis it may be possible to determine whether the populations in the eastern basin are genetically related to UK or French populations.

4.5 Conclusion

The purpose of this study was to understand how new populations of *Gibbula umbilicalis* in the eastern basin of the English Channel compare with longer established sites in the western basin. The presence of juveniles (individuals measuring less than 10mm) at all sites is evidence of successful recruitment within the previous 18 months. Juveniles were detected in greater numbers from the beginning of the study in March in the western basin than they were in the east, where juveniles were not as abundant until May. The younger cohorts in the eastern basin consisted of smaller individuals than the west in any one month. The later appearance and delayed growth of the eastern juveniles signals that reproduction in the eastern basin occurs later than the west, but an accompanying delay to the end of summer fall in sea

temperature in the east is beneficial in reducing post-settlement mortality, which would most likely be greater if temperature drops occurred sooner as they do in the west. The presence of multiple cohorts demonstrates that the populations are not composed of a single generation.

The populations at Cuckmere and Eastbourne may have represented, for a short time, the geographical edge of range for *Gibbula umbilicalis,* but the species is now present in locations further east along the Channel. On this basis, and with evidence of recent recruitment, on-going reproduction and population characteristics comparable to long-term established sites, the species should now be considered established in the eastern basin of the Channel on the English coast.

5. Final Conclusion

The eastward range extension of *Gibbula umbilicalis* is likely a result of a combination of factors, all influenced by sea temperature; increased summer sea temperatures may have accelerated gonad development and spawning, allowing more time for settling animals to grow before winter and thus reduce juvenile mortality. However, although summer temperatures have previously been in the tolerable range, this would have not made a difference in locations where *Gibbula umbilicalis* was absent and it was the change in winter temperatures that facilitated the extension. Winter sea temperatures in the Channel are now milder than they were previously, and at the eastern end of the Channel this has all-but removed temperature as a barrier to recruitment, other than occasional cold winters associated with the proximity to the cooler North Sea. Milder winters increase recruitment success. Populations at the previous edge of range on the Isle of Wight may have increased in size in response to the temperature changes. Increased larval output by these expanding populations may have allowed the barrier to be penetrated and new sites seeded. Since then, recruitment at the new sites has succeeded to such an extent that the populations there are more resilient to failures, fully established and not showing the usual traits of being edge of range populations (failed recruitment).

6. Further Study

With limited time available to collect data for this study only seven consecutive months could be included, and although an understanding of oocyte development could be gained during this period, only two of the four populations had begun to spawn when field work finished. A longer (at least 12 months) repeat of this study would capture a complete reproductive cycle at all sites.

Some aspects of *Gibbula umbilicalis* reproduction have been better studied than others, but one particular area of importance where a knowledge gap exists is that of the duration of the larval phase following spawning. A laboratory study could reveal how long this stage lasts and the results would be beneficial in trying to predict future range extensions, by being able to more accurately predict the distance that larvae can travel.

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Appendices

Appendix A: Results of the 2-tailed Pearson bivariate correlation to test for a significant correlation between shell width and oocyte size. .

Correlations[a]

		MBD	Mean Oocyte
MBD	Pearson Correlation	1	.143
	Sig. (2-tailed)		.436
	N	32	32
Mean Oocyte	Pearson Correlation	.143	1
	Sig. (2-tailed)	.436	
	N	32	32

a. Month = September

Appendix B: Raw ANOVA output from SPSS.

OOCYTE
Tukey HSD

Survey	(I) LOCATION	(J) LOCATION	Mean Difference (I-J)	Std. Error	Sig.
1	Lyme Regis	Osmington	-59.625*	3.526	.000
		Cuckmere	34.048*	3.730	.000
		Eastbourne	34.798*	3.730	.000
	Osmington	Lyme Regis	59.625*	3.526	.000
		Cuckmere	93.673*	3.315	.000
		Eastbourne	94.423*	3.315	.000
	Cuckmere	Lyme Regis	-34.048*	3.730	.000
		Osmington	-93.673*	3.315	.000
		Eastbourne	.750	3.532	.997
	Eastbourne	Lyme Regis	-34.798*	3.730	.000
		Osmington	-94.423*	3.315	.000
		Cuckmere	-.750	3.532	.997

*. The mean difference is significant at the 0.05 level.

Survey	(I) LOCATION	(J) LOCATION	Mean Difference (I-J)	Std. Error	Sig.
2	Lyme Regis	Osmington	-10.961	3.872	.026
		Cuckmere	30.953*	3.992	.000
		Eastbourne	59.302*	4.438	.000
	Osmington	Lyme Regis	10.961*	3.872	.026
		Cuckmere	41.914*	3.928	.000
		Eastbourne	70.263*	4.380	.000
	Cuckmere	Lyme Regis	-30.953*	3.992	.000
		Osmington	-41.914*	3.928	.000
		Eastbourne	28.348*	4.486	.000
	Eastbourne	Lyme Regis	-59.302*	4.438	.000
		Osmington	-70.263*	4.380	.000
		Cuckmere	-28.348*	4.486	.000
3	Lyme Regis	Osmington	1.976	2.337	.833
		Cuckmere	-2.268	2.531	.807
		Eastbourne	-4.056	2.280	.286
	Osmington	Lyme Regis	-1.976	2.337	.833
		Cuckmere	-4.244	2.492	.324
		Eastbourne	-6.032*	2.237	.037
	Cuckmere	Lyme Regis	2.268	2.531	.807
		Osmington	4.244	2.492	.324
		Eastbourne	-1.788	2.439	.884
	Eastbourne	Lyme Regis	4.056	2.280	.286
		Osmington	6.032*	2.237	.037
		Cuckmere	1.788	2.439	.884
4	Lyme Regis	Osmington	-4.088	1.652	.066
		Cuckmere	4.938*	1.652	.016
		Eastbourne	-2.725	1.652	.352
	Osmington	Lyme Regis	4.088	1.652	.066
		Cuckmere	9.025*	1.652	.000
		Eastbourne	1.363	1.652	.843
	Cuckmere	Lyme Regis	-4.938*	1.652	.016
		Osmington	-9.025*	1.652	.000
		Eastbourne	-7.662*	1.652	.000
	Eastbourne	Lyme Regis	2.725	1.652	.352
		Osmington	-1.363	1.652	.843
		Cuckmere	7.662*	1.652	.000
5	Lyme Regis	Osmington	5.400*	1.815	.017
		Cuckmere	9.625*	1.815	.000
		Eastbourne	-4.900*	1.815	.037

*. The mean difference is significant at the 0.05 level.

Survey	(I) LOCATION	(J) LOCATION	Mean Difference (I-J)	Std. Error	Sig.
5	Osmington	Lyme Regis	-5.400	1.815	.017
		Cuckmere	4.225	1.815	.094
		Eastbourne	-10.300*	1.815	.000
	Cuckmere	Lyme Regis	-9.625*	1.815	.000
		Osmington	-4.225	1.815	.094
		Eastbourne	-14.525*	1.815	.000
	Eastbourne	Lyme Regis	4.900*	1.815	.037
		Osmington	10.300*	1.815	.000
		Cuckmere	14.525*	1.815	.000
6	Lyme Regis	Osmington	-7.688*	1.656	.000
		Cuckmere	-5.375*	1.656	.007
		Eastbourne	-6.563*	1.656	.001
	Osmington	Lyme Regis	7.688*	1.656	.000
		Cuckmere	2.313	1.656	.503
		Eastbourne	1.125	1.656	.905
	Cuckmere	Lyme Regis	5.375*	1.656	.007
		Osmington	-2.313	1.656	.503
		Eastbourne	-1.188	1.656	.890
	Eastbourne	Lyme Regis	6.563*	1.656	.001
		Osmington	-1.125	1.656	.905
		Cuckmere	1.188	1.656	.890
7	Lyme Regis	Osmington	-2.127	1.593	.541
		Cuckmere	-3.740	1.593	.090
		Eastbourne	-2.865	1.593	.276
	Osmington	Lyme Regis	2.127	1.593	.541
		Cuckmere	-1.613	1.583	.739
		Eastbourne	-.738	1.583	.966
	Cuckmere	Lyme Regis	3.740	1.593	.090
		Osmington	1.613	1.583	.739
		Eastbourne	.875	1.583	.946
	Eastbourne	Lyme Regis	2.865	1.593	.276
		Osmington	.738	1.583	.966
		Cuckmere	-.875	1.583	.946

*. The mean difference is significant at the 0.05 level.

Appendix C: Mean Oocyte Diameters (µm) for each development stage.

stage	Mean	N	Std. Deviation	Range
2	59.2500	4	19.36276	35.00
3	141.9167	12	14.68121	54.00
4	148.5000	6	8.36062	21.00
5	153.2500	4	3.86221	8.00
6	149.5000	2	2.12132	3.00